BULLETIN

OF

ENTOMOLOGICAL RESEARCH.

ISSUED BY THE COMMONWEALTH
INSTITUTE OF ENTOMOLOGY

EDITOR: THE DIRECTOR

VOL. 46.

LONDON:

COMMONWEALTH INSTITUTE OF ENTOMOLOGY,
56, QUEEN'S GATE, S.W.7.
1956.

A

Commonwealth Agricultural Bureaux.

Executive Council.

J. E. C. Coventry, B.A., M.Sc., *Chairman*, Federation of Rhodesia and Nyasaland.
C. E. Lambert, C.M.G., *Vice-Chairman*, Colonial Territories.
W. C. Tame, United Kingdom.
J. G. Malloch, M.B.E., Ph.D., *Acting*, Canada.
W. Ives, M.Ec., Australia.
V. Armstrong, B.Sc., Ph.D., D.I.C., New Zealand.
E. D. Andrews, *Acting*, Union of South Africa.
T. Swaminathan, I.C.S., India.
Vacant, Pakistan.
V. A. Nicholas, M.B.E., Ceylon.
Sir Herbert Howard, *Secretary*, Farnham House, Farnham Royal, nr. Slough, Bucks.

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

Director and Editor.

W. J. Hall, C.M.G., M.C., D.Sc.

Assistant Director.

E. O. Pearson, B.A.

Head Office—c/o British Museum (Natural History), Cromwell Road, London, S.W.7.
Publication Office and Library—56, Queen's Gate, London, S.W.7.

CONTENTS.

PAGE

ALLEN, M. D. & SELMAN, I. W.
Egg-production in the Mustard Beetle, *Phaedon cochleariae* (F.) in Relation to Diets of Mineral-deficient Leaves (*illustrated*) .. 393

VAN ASPEREN, K.
Toxicity and Interaction of Stereo-isomers of Benzene Hexachloride in Cockroaches (*illustrated*) 837

BANKS, C. J.
An Ecological Study of Coccinellidae (Col.) associated with *Aphis fabae* Scop. on *Vicia faba* (*illustrated*) 561

BARLOW, F. & HADAWAY, A. B.
Studies of Aqueous Suspensions of Insecticides. Part V. The Sorption of Insecticides by Soils 547

BROWN, E. S.
Pseudotheraptus wayi, a new Genus and Species of Coreid (Hemiptera) injurious to Coconuts in East Africa (*illustrated*) .. 221

BURGES, H. D.
Some Effects of the British Climate and Constant Temperatures on the Life-cycle of *Ephestia cautella* (Walker) (*illustrated*) 813

BURSELL, E.
Experiments in Tsetse Control in southern Tanganyika (*illustrated*) 589

BURT, P. E. & WARD, J.
The Persistence and Fate of DDT on Foliage. I.—The Influence of Plant Wax on the Toxicity and Persistence of Deposits of DDT Crystals (*illustrated*) 39

CAMERON, E.
On the Parasites and Predators of the Cockroach. I.—*Tetrastichus hagenowii* (Ratz.) (*illustrated*) 137

CHAUDHRY, GHULAM-ULLAH.
The Development and Fecundity of the Oriental Fruit Moth, *Grapholitha* (*Cydia*) *molesta* (Busck) under Controlled Temperatures and Humidities (*illustrated*) 869

COOMBS, C. W. & FREEMAN, J. A.
The Insect Fauna of an empty Granary (*illustrated*) 399

DAVEY, J. T.
A Method of Marking Isolated Adult Locusts in Large Numbers as an Aid to the Study of their Seasonal Migrations 797

DE LOTTO, G.
Three new Coccids (Hemipt.: Coccoidea) attacking Coffee in East Africa (*illustrated*) 267

CONTENTS.

PAGE

DUNN, J. A. & WRIGHT, D. W.
Population Studies of the Pea Aphid in East Anglia (*illustrated*) .. 369

DUNN, J. A. & WRIGHT, D. W.
Overwintering Egg Populations of the Pea Aphid in East Anglia (*illustrated*) 389

GEERING, Q. A.
A Method for Controlled Breeding of Cotton Stainers, *Dysdercus* spp. (Pyrrhocoridae) (*illustrated*) 743

GILLETT, J. D.
Variation in the Hatching-response of *Aëdes* Eggs (Diptera: Culicidae) (*illustrated*) 241

GILLETT, J. D.
The Inherited Basis of Variation in the Hatching-response of *Aëdes* Eggs (Diptera: Culicidae) 255

GLOVER, P. E., JACKSON, C. H. N., ROBERTSON, A. G. & THOMSON, W. E. F.
The Extermination of the Tsetse Fly, *Glossina morsitans* Westw., at Abercorn, Northern Rhodesia (*illustrated*) 57

GRUNBERG, A., POLAC'EK, K. & PELEG, J.
Fumigation Trials with Ethylene Dibromide for the Control of Eggs and Larvae of *Ceratitis capitata* (Wied.) in *Citrus* Fruit 803

HADAWAY, A. B.
The Biology of the Dermestid Beetles, *Trogoderma granarium* Everts and *Trogoderma versicolor* (Creutz.) (*illustrated*) 781

HADDOW, A. J.
Observations on the Biting-habits of African Mosquitos in the Genus *Eretmapodites* Theobald (*illustrated*) 761

HANNA, A. D., JUDENKO, E. & HEATHERINGTON, W.
Systemic Insecticides for the Control of Insects transmitting Swollen-shoot Virus Disease of Cacao in the Gold Coast (*illustrated*) 669

HOWE, R. W. & BURGES, H. D.
Trogoderma afrum Priesner, a Synonym of *T. granarium* Everts and a Comparison with *T. versicolor* (Creutz.) (*illustrated*) 773

HOWE, R. W. & FREEMAN, J. A.
Insect Infestation of West African Produce imported into Britain (*illustrated*) 643

IYENGAR, M. O. T. & MENON, M. A. U.
Mosquitos of the Maldive Islands (*illustrated*) 1

JACKSON, C. H. N.
The Pattern of *Glossina morsitans* Communities (*illustrated*) .. 517

KEMP, P. B.
The Termites of north-eastern Tanganyika; their Distribution and Biology (*illustrated*) 113

CONTENTS.

PAGE

KENTEN, J.
The Effect of Photoperiod and Temperature on Reproduction in *Acyrthosiphon pisum* (Harris) and on the Forms produced (*illustrated*) 599

KIRKLAND, R. C. & STYLES, J. H.
Notes on *Pristiphora glauca* Benson (*illustrated*) 749

LAIRD, M.
Abnormalities exhibited by Mosquito Larvae collected in Tonga (*illustrated*) 185

LAIRD, M.
Mosquitos and Malaria in the Hill Country of the New Hebrides and Solomon Islands (*illustrated*) 275

LAIRD, M.
Notes on the Mosquitos of the Gilbert, Ellice and Tokelau Islands, and on Filariasis in the latter Group (*illustrated*) 291

LEESON, H. S.
Further Notes on the Geographical Distribution of Old World Species of *Ornithodoros* (Acarina) 747

LUMSDEN, W. H. R.
Entomological Studies, relating to Yellow Fever Epidemiology, at Gede and Taveta, Kenya (*illustrated*) 149

MATTINGLY, P. F. & BROWN, E. S.
The Mosquitos (Diptera: Culicidae) of the Seychelles (*illustrated*) 69

MILES, M.
Studies of British Anthomyiid Flies. VI.—The annual Cycle of Generations in some Anthomyiid Root Flies 11

MILES, M.
Studies of British Anthomyiid Flies. VII.—The Onion-Fly Complex 21

MORISON, G. D., JEFFREE, E. P., MURRAY, L. & ALLEN, M. D.
Acarine and *Nosema* Diseases of Honeybees in Britain, 1925-47 (*illustrated*) 753

NAIDU, MOHAN BABU.
Physiological Action of Drugs and Insecticides on Insects (*illustrated*) 205

NASH, T. A. M.
A Note on the Parasitisation of the Oöthecae of *Periplaneta americana* (L.) by the Chalcid, *Syntomosphyrum glossinae* Wtstn. 111

NASH, T. A. M.
The Fertilisation of *Glossina palpalis* in Captivity (*illustrated*) .. 357

NOTLEY, F. B.
The *Leucoptera* Leaf Miners of Coffee on Kilimanjaro. II.—*Leucoptera caffeina* Wshbn. (*illustrated*) 899

PARKIN, E. A. & BILLS, G. T.
Insecticidal Dusts for the Protection of Stored Peas and Beans against Bruchid Infestation (*illustrated*) 625

CONTENTS.

PAGE

PITCHER, R. S.
A Comparison of a Group of Gall Midges of the Genus *Thomasiniana* Strand, E. 1916 and a Description of a new Species from wild Blackberry (*illustrated*) 27

POTTER, C., HEALY, M. J. R., & RAW, F.
Studies on the Chemical Control of Wireworms (*Agriotes* spp.). I.—The Direct and Residual Effects of BHC, DDT, D-D, and Ethylene Dibromide (*illustrated*) 913

SALITERNIK, Z.
The specific Biological Characteristics of *Anopheles* (*Myzomyia*) *sergentii* (Theo.) and their Correlation with Malaria Control in Israel (*illustrated*) 445

SALT, G.
The Arthropod Population of the Soil under Elephant Grass in Uganda 539

SMITH, A.
The Transmission of Bancroftial Filariasis on Ukara Island, Tanganyika. I.—A Geographical and Ecological Description of the Island with an annotated List of Mosquitos and other Arthropods of medical Importance (*illustrated*) 419

SMITH, A.
The Transmission of Bancroftial Filariasis on Ukara Island, Tanganyika. II.—The Distribution of Bancroftial Microfilaraemia compared with the Distribution of Hut-haunting Mosquitos and their Breeding Places (*illustrated*) 437

SMITH, A.
The Transmission of Bancroftial Filariasis on Ukara Island, Tanganyika. III.—Biting-incidences on Man and Filarial Infections in wild caught Mosquitos 495

SMITH, A.
The Transmission of Bancroftial Filariasis on Ukara Island, Tanganyika. IV.—Host-preferences of Mosquitos and the Incrimination of *Anopheles gambiae* Giles and *A. funestus* Giles as Vectors of Bancroftial Filariasis 505

SOLOMON, M. E.
The relative Control Values of different Percentage Mortalities (*illustrated*) 189

SOLOMON, M. E. & ADAMSON, B. E.
The Powers of Survival of Storage and Domestic Pests under Winter Conditions in Britain (*illustrated*) 311

SOUTHWOOD, T. R. E.
The Nomenclature and Life-cycle of the European Tarnished Plant Bug, *Lygus rugulipennis* Poppius (Hem., Miridae) 845

TEESDALE, C.
Studies on the Bionomics of *Aëdes aegypti* (L.) in its Natural Habitats in a Coastal Region of Kenya (*illustrated*) 711

PAGE

van Someren, E. C. C., Teesdale, C. & Furlong, M.
The Mosquitos of the Kenya Coast; Records of Occurrence, Behaviour and Habitat 463

Ward, J. & Burt, P. E.
The Persistence and Fate of DDT on Foliage. II.—Comparative Rates of Loss of DDT Deposits from Glass Plates and Growing Leaves (*illustrated*) 849

Weitz, B. & Jackson, C. H. N.
The Host-animals of *Glossina morsitans* at Daga-Iloi 531

Wharton, R. H.
The Susceptibility of various Species of Mosquitos to DDT, Dieldrin and BHC 301

Williams, C. B., French, R. A. & Hosni, M. M.
A second Experiment on testing the relative Efficiency of Insect Traps (*illustrated*) 193

Dates of Publication in Parts

Part I	pp. 1–240	..	29 April 1955
Part II	pp. 241–462	..	29 August 1955
Part III	pp. 463–742	..	25 October 1955
Part IV	pp. 743–923	..	6 January 1956

Errata

Page 29, 3 lines from end, for " tabulated above " read " in Table III " ; transfer sentence " In addition to the data . . . quince." to page 30, line 4 and insert after " from time to time."
Page 30, line 12, for " tabulated above " read " in Table V "
Page 53, 12 lines from end, for " temperature " read " temperate "
Page 115, Table I, line 7 for " *Crenitermes* " read " *Crenetermes* "
Page 308, line 6, for " *Anopheles albopictus* " read " *Aë. albopictus* "
Page 327, lines 2 and 3, for " (Pl. XI, fig. 5) " read " (Pl. XII, fig. 1) "
Page 335, lines 26–29, transfer paragraph " This species must develop . . . at 20°C." to page 339, and insert under *Oryzaephilus surinamensis* after paragraph ending " of their origin."
Page 440, Table II, last col., totals, for " 2,79 " read " 2,793 "
Page 579, 14 lines from end, for " examined " read " examination "
Page 689, line 35, for " designed " read " designed and carried out jointly with the West African Cacao Research Institute "
Page 691, Table XXII, last col., for " 15·5 " read " 10·6 "
Page 692, line 1, for " 15·5 " read " 10·6 "
Page 697, line 3, for " 1951 " read " 1951 and was carried out jointly with the West African Cacao Research Institute "
Page 708, line 16, for " 0·1 " read " 0·01 "; 5 lines from end, for " 0·08 " and " 15·5 " read " 0·1 " and " 10·6 " respectively
Page 811, line 21, for " 96·4 " read " 100 "

COMMONWEALTH INSTITUTE OF ENTOMOLOGY.

BULLETIN
OF
ENTOMOLOGICAL RESEARCH.

Vol. 46. 1955.

MOSQUITOS OF THE MALDIVE ISLANDS.

Abd-
Capt. Rud

By M. O. T. Iyengar and M. A. U. Menon.

With an Appendix by P. F. Mattingly, *British Museum (Natural History)*.

The Maldives are coral islands in the Indian Ocean, to the south-west of Ceylon. Covell (1944) reported the occurrence of *Anopheles tessellatus* Theo., and Carter & Wijesundara (1948) recorded three Culicines, *Culex sitiens* Wied., *C. tritaeniorhynchus* Giles and *C. stylifurcatus* Carter & Wijesundara (*spathifurca* Edw.), from Addu, the southernmost atoll of the Maldives.

The authors made a large collection of mosquitos from islands in five atolls of the Maldives, namely, Malé, Kolumadulu, Haddumatti, Suvadiva and Addu. Iyengar (1952), after a preliminary examination of the collection, listed 13 species which include the four species previously recorded. As a result of further study made of this material, it is now known that 15 species of mosquitos occur in the Maldives, as listed below.

Culicini:

1. *Harpagomyia genurostris* Leic.
2. *Armigeres* (*Armigeres*) *obturbans* (Wlk.)
3. *Aëdes* (*Stegomyia*) *aegypti* (L.)
4. *Aëdes* (*Stegomyia*) *albopictus* (Skuse)
5. *Aëdes* (*Stegomyia*) sp. in *scutellaris* (Wlk.) group
6. *Culex* (*Lophoceraomyia*) *minutissimus* (Theo.)
7. *Culex* (*Lophoceraomyia*) *infantulus* Edw.
8. *Culex* (*Mochthogenes*) *malayi* (Leic.)
9. *Culex* (*Culiciomyia*) *spathifurca* Edw.
10. *Culex* (*Culex*) *tritaeniorhynchus* Giles
11. *Culex* (*Culex*) *vishnui* Theo.
12. *Culex* (*Culex*) *sitiens* Wied.
13. *Culex* (*Culex*) *pipiens fatigans* Wied.

Anophelini:

14. *Anopheles* (*Myzomyia*) *subpictus* Grassi
15. *Anopheles* (*Myzomyia*) *tessellatus* Theo.

Notes of taxonomic interest on some of these species are furnished below.

Aëdes aegypti (L.) (fig. 1).

Larva.

A number of specimens showed a single pecten tooth well separated from the main rank of the pecten and placed posterior to the siphonal hair (fig. 1 a). In the majority of the specimens, however, this feature was absent. Barraud (1934, p. 245) considered that the occurrence of one, occasionally two, pecten teeth well separated from the rank of the pecten was an exclusive character of *Aëdes* (*Stegomyia*) *vittatus* (Big.) not observed in any other known larvae of the subgenus *Stegomyia*. The occurrence of an isolated pecten tooth in *A. aegypti*, though only an occasional variation, would indicate that this feature is not confined to *A. vittatus* alone. It would appear that the occurrence of this feature in *A. aegypti* is not uncommon in other parts of the world, as evidenced by the fact that the figure of the larva by Ross & Roberts (1943) shows the isolated pecten tooth clearly.

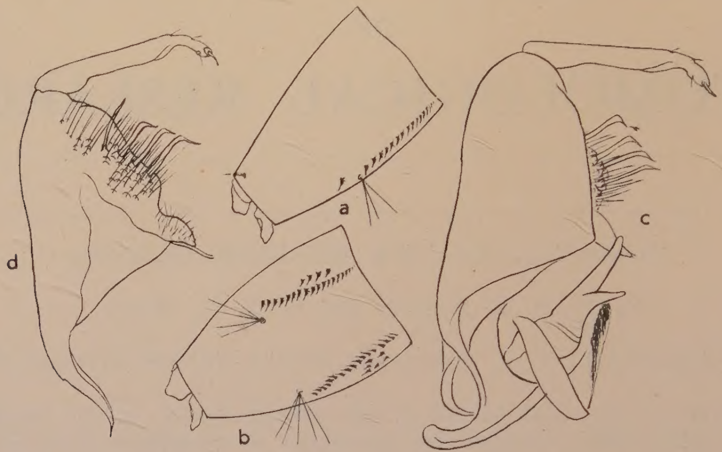


Fig. 1.—*Aëdes* (*Stegomyia*) *aegypti*. (a) larval siphon (lateral view) showing distal tooth of pecten separated from the main rank and placed posterior to the siphonal hair; (b) larval siphon (dorsal view) showing a rare variation in which the pecten has an accessory series of teeth placed ventrally to the main rank; (c) hypopygium of male, true ventral view of left half; (d) true dorsal view of coxite showing the distinctive "elbowed" spines on the basal lobe.

Another variation of the pecten, though very rare, is the occurrence of an additional irregular series of four to seven pecten teeth placed ventrally to the main rank (fig. 1 b).

Adult.

As regards palpal and tarsal ornamentation, the specimens from the Maldives conform to the type form described by Barraud (1934). The male hypopygium in these specimens, however, shows a constant difference from that figured by Barraud (*l.c.*, p. 222). The spines arising from the basal lobe of the coxite are figured as straight, pointed and about equal in size. In all the specimens from the Maldives, there occur on the basal lobe of the coxite, in addition to the straight spines and numerous hairs in that situation, a number (3 or 4) of distinctive spines which are thicker and better developed than the others, and are conspicuously elbowed close to apex (fig. 1 c & d). In this respect, the Maldives specimens conform to the figure given by Ross & Roberts (1943) of the male terminalia.

Aëdes albopictus (Skuse) (fig. 2).

Larva.

According to Barraud (1934), frontal hair B is usually single. In the Maldives series this hair is distinctly bifid, the bifurcation starting at about a third from base. The two branches are often approximated, thus giving the impression that the hair is single; a closer examination reveals its bifid character. In a solitary specimen, this hair was single on one side and bifid on the other. Specimens from India also showed that the frontal hair B was bifid.

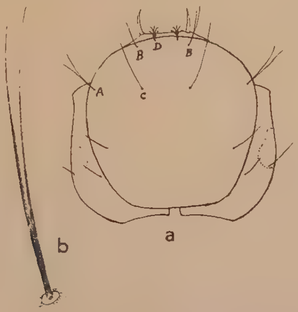


Fig. 2.—*Aëdes* (*Stegomyia*) *albopictus.* (a) head of larva showing frontal hairs A, B, C and D; (b) frontal hair B (enlarged view).

The inner submedian caudal hair, according to Barraud, is single or split into two. In several specimens from the Maldives, this hair is distinctly 3-branched.

The siphonal hair, according to Barraud, is 2- to 3-branched. In specimens from the Maldives, this hair generally has 3, sometimes 4, branches; it is never bifid.

Aëdes sp. in **scutellaris** (Wlk.) group (fig. 3).

Among a number of adult *A. albopictus* bred from larvae collected from leaf-bases of *Alocasia indica*, there was a solitary male specimen resembling *Aëdes andrewsi* Edw. The ornamentation on the pleurae is obscure, as the specimen is badly denuded. The hypopygium resembles that of *A. andrewsi* in the following characters mentioned by Edwards (1926): "Side piece 3·5 × 1. Basal lobe large, tip rather rounded and densely hairy; dorsal hairs long, ventral hairs shorter and denser. Clasper moderately stout and slightly swollen at tip; spines stout, blunt and slightly curved." In addition to these characters, this specimen shows another important character figured by Edwards, though not mentioned in the text, namely the occurrence of a group of stout spines at the apex of the basal lobe of the coxite. In the Maldives specimen, this characteristic feature is conspicuous and there are four large flattened lanceolate spines arising from the apex of the basal lobe (fig. 3 a & b). Differences from *A. andrewsi* are noted by Mr. Mattingly in the accompanying Appendix (p. 9).

A. andrewsi had been previously recorded only from the Christmas Islands to the south of Java.

Culex minutissimus (Theo.).

The larva of this species is readily recognised by the presence of two dark bands on the siphon, one at base and one at middle of the siphon (fig. 4 f). In the 4th-instar larva, frontal hairs B and C are both 2-branched, although in the earlier instars they are single. Prothoracic pleural hairs 1–3, which arise from a common chitinous plate, are not all of the same size; hairs 1 and 2 are very long and of about equal length, while hair no. 3, which is single or bifid, is very short and about a third of the other hairs. This feature appears to be characteristic of all the species of *Lophoceraomyia* but it is not restricted entirely to this subgenus. This feature, namely prothoracic pleural hairs 1 and 2 being long and hair 3 being short, has been observed in one other species, *Culex* (*Neoculex*) *brevipalpis* (Giles). In subgenus *Culex*, all the propleural hairs 1 to 3 are of nearly equal length.

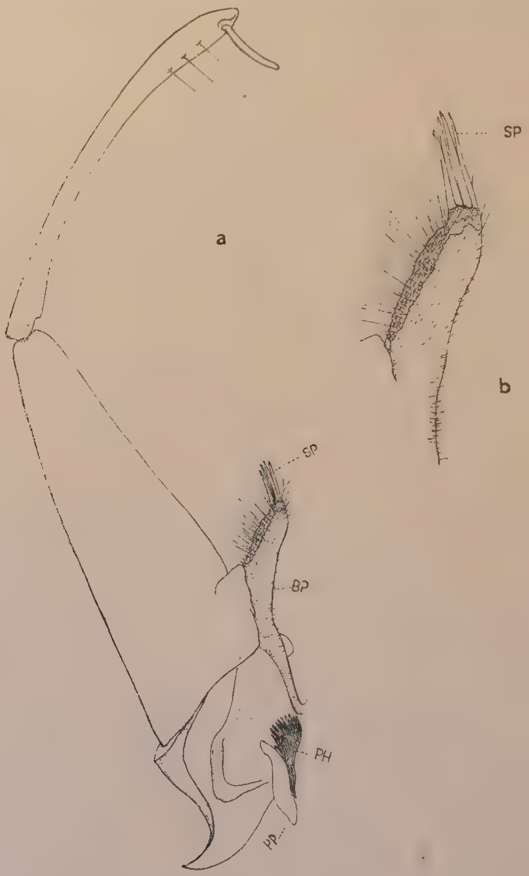


Fig. 3.—*Aëdes* (*Stegomyia*) sp. in *scutellaris* group. (a) left half of male hypopygium (true ventral view) showing the characteristic spines (SP) at the apex of the basal lobe (BP) of coxite; PH, phallosome; PP, parameral plate; (b) enlarged view of the basal lobe of coxite.

Lateral hair on abdominal segment II is invariably 3-branched, the foremost branch being shorter than the other two. The pecten in the Maldives specimens consist of 13 to 16 teeth.

The inner submedian caudal hair, as shown by Barraud, has usually 4 branches, one very long and three short ones, the longest being always the third from above. Usually in the other subgenera of *Culex*, and generally in other species of mosquitos where the inner submedian caudal hair has several branches, the branches are more or less of equal size. Where, however, they are of different sizes, there occurs a progressive increase in length from the uppermost to the lowermost.

The form of *C. minutissimus* found in the Maldives does not differ materially from the description given by Barraud (1934) which is based on that by Senior White (1927). The minor differences noted may possibly be due to Senior White's description being based on 3rd-instar larvae, while the present notes are based on a study of 4th-instar larvae.

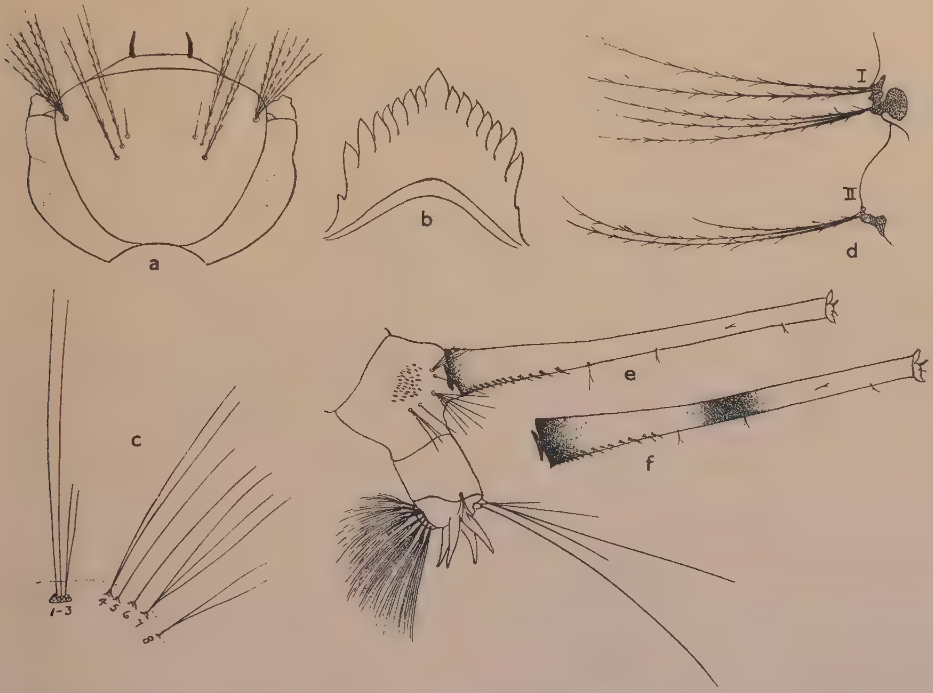


Fig. 4.—Larval structures of *Culex* (*Lophoceraomyia*) *infantulus* ((a) to (e)) and of *C.* (*L.*) *minutissimus* (f). (a) head; (b) mentum; (c) dorsum of thorax (right side) showing prothoracic pleural hairs nos. 1 to 8; (d) lateral hairs of abdominal segments I and II; (e) tail end; (f) larval siphon of *C.* (*L.*) *minutissimus*.

Culex infantulus Edw. (fig. 4 a to e).

Adults of this species collected from the Maldives do not show any variation from the form originally described (as *parainfantulus* Menon) by Menon (1944) from the mainland of India.

The larva of *C. infantulus* is very similar to that of *C. minutissimus* and does not show any outstanding difference from the latter as regards chaetotaxy. A difference was noted in regard to the dark band at the middle of the siphon. The larva of *C. minutissimus* has a well-marked dark band at the middle of the siphon (fig. 4 f). This dark band is either totally wanting in *C. infantulus*, or only faintly visible.

The following is a description of the important features of the larva of the Maldive Islands form of *C. infantulus*:

Pre-clypeal spines dark, straight and pointed. Frontal hair A with 6 subplumose branches; frontal hairs B and C, each of 2 long subplumose branches. Hair *d* anterior and internal to B and C, fine, thin and single. Mentum with rather large median tooth and 7 to 8 teeth on either side.

Prothoracic pleural hairs 1 and 2, long and single, hair 3 short and bifid, hair 4 of two branches, hairs 5 and 6 single, hair 7 of three branches and hair 8 of two branches.

Abdominal segment I has two long lateral hairs, one of which is two-branched and the other three-branched. Segment II with a three-branched lateral hair, the foremost branch being short and about half the length of the other branches.

Siphon long and narrow, 8 times length of diameter at base, with a faint dark band at base. Dark band at middle of siphon absent or only feebly indicated. Subsiphonal hair 6–7-branched, branches not plumose.

Anal segment: lateral hair 4-branched. ISC 4-branched, the third branch from above being the longest, OSC long and single. Papillae about two-thirds length of anal segment, narrow and pointed.

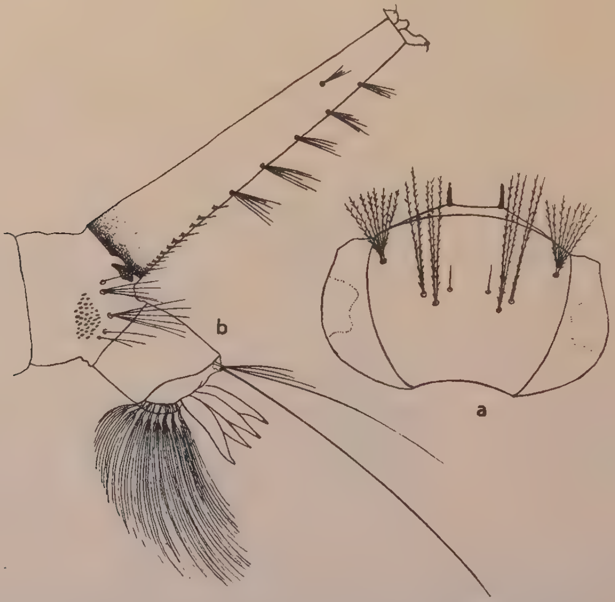


Fig. 5.—Larval structures of *Culex* (*Culex*) *tritaeniorhynchus*. (a) head; (b) tail end.

Culex tritaeniorhynchus Giles (fig. 5).

Larva.

Frontal hair B ordinarily 3-branched and hair C, two-branched. Sometimes, frontal hair B has 2 branches on one side and 3 on the other, and very rarely two branches on either side. In the last mentioned condition, there is the possibility of such a specimen being mistaken for *Lophoceraomyia*. In the latter subgenus, as previously mentioned, prothoracic pleural hair 3 is poorly developed and much smaller than hairs 1 and 2.

Barraud mentions two forms of *C. tritaeniorhynchus*, based mainly on the length of the siphon, the type form with a comparatively short siphon (index about 5) and the other with a longer siphon (index about 8). Martini's (1931) description of the species refers to the latter form. Carter & Wijesundara (1948) mention the occurrence of these two forms in Ceylon as well as in the Maldives. A study of the material from the Maldives shows that the two forms represent the extreme limits of normal variation in the length of the siphon and that intermediate forms occur which bridge the two extreme conditions. This may be seen from Table I, which gives the siphonal indices of 17 larvae of *C. tritaeniorhynchus* studied from a single locality in the Maldives.

TABLE I.

Variations in the siphonal index of larvae of *C. tritaeniorhynchus*.

Siphonal index	4·75–5·0	5·25–6·0	6·5–7·0	7·25–7·5
Number of specimens	3	8	5	1

Adult.

Carter & Wijesundara (1948) mention that there are two distinct forms of *C. tritaeniorhynchus* in the Maldives, (a) a form in which the pale band on the proboscis extends ventrally towards the base or on to the sides or dorsal surface, and (b) that in which the pale band on the proboscis is sharply defined and restricted both dorsally and ventrally to the middle region of the proboscis. The present observations based on the examination of a large number of specimens from the Maldives show that, while the extreme forms correspond to the two types mentioned by Carter & Wijesundara, there are numerous specimens showing intermediate stages between the form with a well-defined band at the middle of the labium and that in which the pale band extends to the base of the labium. Even in the form with a clear-cut band, there are indications of pale scaling scattered on the ventral aspect, suggesting the extension of the band. In view of the wide variations observed and the occurrence of intermediate forms, this species cannot possibly be grouped into two distinct forms as suggested by Carter & Wijesundara.

Culex sitiens Wied. (fig. 6).

Larva.

The siphonal index in this species varies considerably in different regions (*vide* Cooling, 1924; Hopkins, 1952; Lee, 1944). The Indian form (Barraud, 1934) has the smallest index of 2 to 2·5, while the Australian form has a siphonal index of 5·5 (Lee, *loc. cit.*). Carter & Wijesundara (1948) found that the siphonal index in *C. sitiens* from the Maldives ranged between 4·2 and 4·5. The present authors have observed specimens of larvae of *C. sitiens* from the same area, with even smaller siphonal indices, the lowest figure recorded being 3·2.

The Indian form, according to Barraud, has five pairs of ventral hair tufts on the siphon, besides the lateral pair. The Maldives specimens showed 6 pairs of ventral hair tufts in addition to the lateral pair.

Another variation observed was in regard to the inner submedian caudal hair. In the Indian form, according to Barraud, this hair is 3-branched. Fourth-instar larvae of this species examined from the Maldives showed that this hair was invariably 4-branched, and sometimes 5-branched (fig. 6 b).

Adult.

The adults from the Maldives differ from the Indian form in having light fawn-coloured scales covering the mesonotum, instead of dark brown scales. The male hypopygium is identical with that of the Indian form, except that the ventral cornua bears numerous short downy hairs on its posterior aspect, giving it a pubescent appearance (fig. 6 c to e). This was first noted by Edwards (1922).

Summary.

A large collection of mosquitos made in five atolls of the Maldive Islands has revealed the presence of 15 species. These are listed and notes of taxonomic interest on seven of them are given.

Acknowledgements.

The authors wish to acknowledge with many thanks the helpful criticism of Mr. P. F. Mattingly.

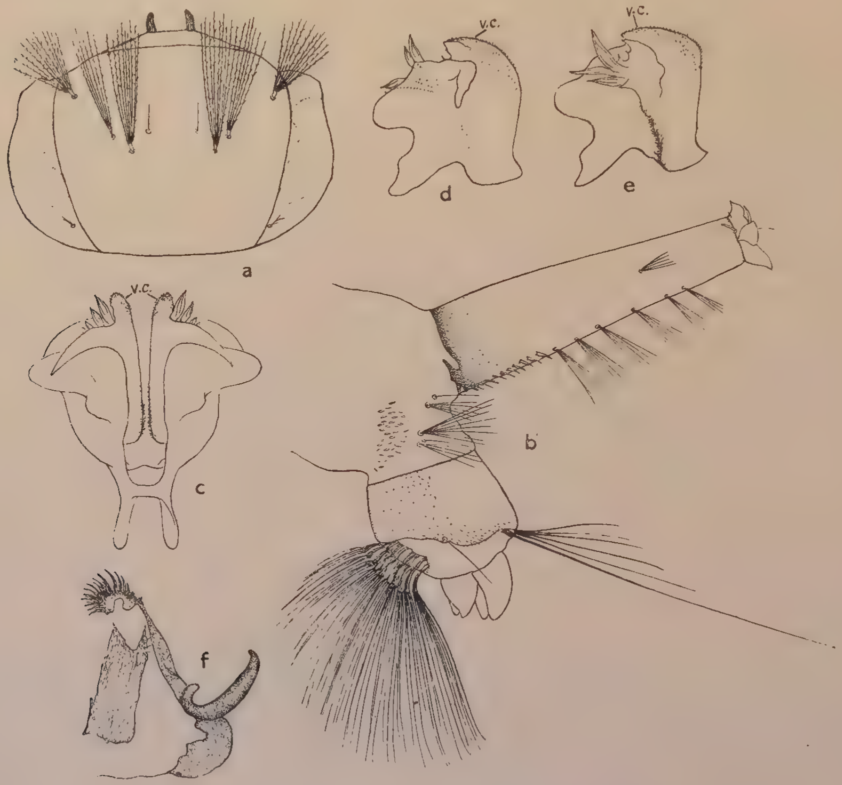


Fig. 6.—*Culex* (*Culex*) *sitiens*. (a) head of larva; (b) tail end of larva; (c) phallosome (full ventral view); (d) and (e) lateral view (flat preparation) of phallosomal plate showing pubescence on ventral cornua (v.c.); (f) paraproct.

References.

Barraud, P. J. (1934). The fauna of British India . . . Diptera. Vol. V. Family Culicidae. Tribes Megarhinini and Culicini.—463 pp. London, Taylor & Francis.

Carter, H. F. & Wijesundara, D. P. (1948). Notes on some Ceylon Culicine mosquitoes.—Ceylon J. Sci., (B) **23**, pp. 135–151.

Cooling. L. E. [1924]. Seven common species of mosquitoes described for purposes of identification.—Serv. Publ. Dep. Hlth Aust. trop. Div., no. 1, 24 pp.

COVELL, G. (1944). Notes on the distribution, breeding places, adult habits and relation to malaria of the Anopheline mosquitoes of India and the Far East.—J. Malar. Inst. India, **5**, pp. 399–434.

EDWARDS, F. W. (1922). A synopsis of adult oriental Culicine (including Megarhinine and Sabethine) mosquitoes.—Indian J. med. Res., **10**, pp. 249–293, 430–474.

EDWARDS, F. W. (1926). Mosquito notes. VI.—Bull. ent. Res., **17**, pp. 101–131.

HOPKINS, G. H. E. (1952). Mosquitoes of the Ethiopian Region. I.—2nd edn., 355 pp. London, Brit. Mus. (Nat. Hist.).

IYENGAR, M. O. T. (1952). Filariasis in the Maldive Islands.—Bull. World Hlth Org., **7**, pp. 375–403.

LEE, D. J. (1944). An atlas of the mosquito larvae of the Australasian region. (Issued by the Australian Military Forces.)

MARTINI, E. (1931). Culicidae. *In* Lindner, E. Die Fliegen der palaearktischen Region, Lief. 53, pp. 321–398.

MENON, M. A. U. (1944). On a new species of the subgenus *Lophoceratomyia* Theobald 1905 (Diptera, Culicidae).—J. Malar. Inst. India, **5**, pp. 389–393.

ROSS, E. S. & ROBERTS, H. R. (1943). Mosquito atlas. Part I.—44 pp. Philadelphia, Pa., Amer. ent. Soc.

SENIOR WHITE, R. (1927). Notes on Ceylon mosquitoes. II.—Spolia zeylan., **14**, pp. 61–76.

APPENDIX.

By P. F. MATTINGLY

British Museum, Natural History.

Dr. Iyengar and Mr. Menon very kindly submitted to me specimens of certain doubtful species from among their collection of mosquitos from the Maldive Islands. I have been particularly glad of the opportunity to examine this material since it is apposite to a recently completed study of the mosquitos of the Seychelles in relation to those of other islands in the western Indian Ocean (Mattingly & Brown, 1955). The new species of the *Aëdes scutellaris* complex is also of special interest for the study of that important group since it is by far the most westerly species yet discovered, the next in order being an undescribed species from the Andaman Islands.

Aëdes (Stegomyia) sp. in **Aëdes scutellaris** (Wlk.) group.

I have described this species in detail elsewhere (Mattingly, 1954). It appears to me to be possibly new to science but I am unwilling to name it until further material is available since it is at present known only from a unique much damaged male adult. It appears to be related to *Aëdes scutellaris* and *A. andrewsi* Edw. It appears to differ from both these species in having pale scales on the underside of the proboscis. Other differences from *A. andrewsi* include the absence of any interruption to the pale band on the 4th hind tarsal and the presence of an interruption to the 1st hind tarsal. The arrangement of modified setae on the basal lobe of the hypopygium appears to be more like that observed in *A. scutellaris* of which, in my view, it may well be a subspecies. It is very likely that one or more of these species will be found to occur in

Indonesia. The precise identity of the species of the *A. scutellaris* group occurring in that area has yet to be established (Marks, 1954).

Culex (Lophoceraomyia) infantulus Edw. (1922).

Mr. Menon kindly sent me a male adult of this species from Fiori, Maldive Is., a whole larva from Addu Atoll, Maldive Is., and a male adult of *Culex parainfantulus* Menon (1944) from Pathanamthitta, Travancore. These specimens are now in the British Museum. I have compared them with the holotype male of *C. infantulus* from Hong Kong and other material of this species from China. I can find no significant difference and I am forced to conclude that, as previously suggested (Mattingly, 1949), *parainfantulus* should be sunk as a synonym of *infantulus*.

Culex (Culiciomyia) spathifurca Edw. (1915).

Mr. Menon sent two male adults and two female adults from Havaru Tinadu, Suvadiva Atoll, Maldive Is., which are now in the British Museum. I have compared these with the description of *Culex stylifurcatus* Carter & Wijesundara from Ceylon given by Carter & Wijesundara (1948) and with the holotype male of *C. spathifurca* from Borneo, and other specimens of this species from Java and Singapore. More recently I have also been able to examine the terminalia of the holotype ♂ of *C. stylifurcatus* which are now in the British Museum, together with those of the types of other species described by Carter & Wijesundara, thanks to the kindness of the Director of Medical Services, Ceylon and of Dr. Wijesundara. I can find no significant difference. I have also compared larvae of *C. spathifurca* from Singapore (described by Edwards, 1926) with the description of their species given by Carter & Wijesundara. Here again I can find no significant difference. It would appear therefore that the name *stylifurcatus* should be sunk as a synonym of *spathifurca*.

Aëdes (Stegomyia) aegypti (L.).

In connection with Iyengar & Menon's interesting note on the detached pecten spines of this species it may be remarked that since Barraud's time it has become apparent that a detached spine or spines normally occur in many Ethiopian species of *Stegomyia* (see Hopkins, 1952).

References.

Edwards, F. W. (1915). Diagnoses of new Bornean Culicidae.—Bull. ent. Res., **5,** pp. 283–285.

Marks, E. N. (1954). A review of the *Aedes scutellaris* subgroup with a study of variation in *Aedes pseudoscutellaris* (Theobald) (Diptera, Culicidae).—Bull. Brit. Mus. (nat. Hist.), Ent. **3,** pp. 349–414.

Mattingly, P. F. (1949). Notes on some oriental mosquitoes.—Proc. R. ent. Soc. Lond., (B) **18,** pp. 219–228.

Mattingly, P. F. (1954). Notes on the subgenus *Stegomyia* (Diptera, Culicidae), with a description of a new species.—Ann. trop. Med. Parasit., **48,** pp. 259–270.

Mattingly, P. F. & Brown, E. S. (1955). The mosquitos (Diptera; Culicidae) of the Seychelles.—Bull. ent. Res., **46,** pp. 69–110.

The other papers to which reference is made are listed by Iyengar & Menon in their bibliography on pp. 8–9.

STUDIES OF BRITISH ANTHOMYIID FLIES.

VI.—THE ANNUAL CYCLE OF GENERATIONS IN SOME ANTHOMYIID ROOT FLIES.

By Mary Miles
Wye College (University of London).

Observations on the biology of the root-infesting Anthomyiid flies, namely, onion fly (*Delia antiqua* (Mg.)), cabbage root fly (*Erioischia brassicae* (Bch.)), turnip root fly (*E. floralis* (Fall.)) and bean seed flies (*D. cilicrura* (Rond.) and *D. trichodactyla* (Rond.)), show that there are marked differences in the times of occurrence and the annual cycle of generations of the several species, and that accurate knowledge of the number of generations, their relative numerical strength and the conditions in which they are active is essential for the interpretation of pathological conditions in the host crops.

Onion Fly (*Delia antiqua* (Mg.)).

Among larvae of onion fly obtained from two centres in the west of England in late June and early July 1952, approximately 20 per cent. entered a pupal diapause which continued until the following spring (Miles, 1953*a*). Maan (1945) also observed that some first-generation pupae overwintered. From the literature, it appeared that the annual cycle of generations of the onion fly had not been determined.

Smith (1922) stated that there appeared to be three generations of onion flies in a season, the third being incomplete, and he constructed what he called an artificial table, based on the observed rate of development of the first generation, to show the approximate times of occurrence of the various stages of the successive generations. He considered that the presence of larvae on onions in September and October was an indication that there were three generations a year, but he thought that the generations were not sharply divided. With regard to the third generation, Maan (*op. cit.*) stated, " if the weather in the latter part of the summer or in autumn is hot a third generation may appear ", but he gave no supporting evidence.

Emergence in spring.

At Wye, pupae that entered the overwintering diapause in July and pupae reared from eggs laid in captivity in July were kept in an insectary during the winter of 1952–53. The flies emerged from 27th April–16th May, with a peak emergence period from 1st–7th May. The offspring of these were bred in captivity, and pupae from both first and second generations of 1953 were overwintered. In 1954, flies emerged from 22nd April–28th May, with a peak emergence period from 5th–13th May. In both seasons the peak emergence period was well defined, approximately 50 per cent. in 1953 and 75 per cent. in 1954 emerging within eight days.

It has not been possible to compare the time of emergence in the insectary with that in the field because the writer has not found a natural infestation at Wye. Smith (*op. cit.*) first observed the flies about onion crops on 30th and 31st May and then in much larger numbers in the early part of June. Maan (*op. cit.*) used traps over infested soil to collect emerging adults, the traps being constructed in such a way that the flies were visible when they assembled on a glass window. Since the flies shelter in the surface soil when the temperature is low they were not visible in the cages until the temperature reached the threshold for normal activity. Maan first found flies in the traps on 21st–23rd May, which can be taken as the time when they first became active, and at three sites in Holland he found that the highest numbers occurred in the second week of June. From the observations of Smith and Maan it can be concluded that there is little activity by onion flies from overwintered pupae until the latter part of May, though it seems likely that emergence may take place somewhat earlier.

Spring egg-laying period.

Smith (*op. cit.*) gave 28th May as the beginning of the spring egg-laying period, and Maan (*op. cit.*) stated that egg-laying began about ten days after the emergence of adults, which he considered to take place from the second half of May to the second half of June, according to the prevailing temperature.

At Wye in 1953, eggs were not seen in the breeding cages until the fourth week of May, when the maximum day temperature out-of-doors was 70–80°F. and the age of the flies varied from 1–4 weeks. In 1954, eggs were first laid in captivity on 13th May, when the maximum day temperature of the laboratory had been 75–84°F. for almost a week and the age of the flies was from one day to three weeks. During the third and fourth weeks of May 1954 the temperatures were much lower, only occasionally exceeding 65°F., and during that time egg-laying virtually ceased. Heavy egg-laying again occurred from 26th–28th May when the day temperatures again exceeded 80°F.

These observations suggested that temperature was a more important factor than age in stimulating oviposition among flies in captivity, and that temperatures of approximately 80°F. were necessary if caged flies were to lay eggs freely. This is 10°F. higher than the temperature required to stimulate oviposition by cabbage root flies in captivity (Miles, 1954). The observed threshold temperature for oviposition for cabbage root flies in the field is approximately 60°F., as indicated by a screened thermometer, and it seems reasonable to conclude by analogy that the corresponding temperature for egg-laying by onion flies in the field is about 10°F. higher, that is, approximately 70°F. Confirmatory evidence of the need of onion flies for high temperatures is provided by the fact that the normal period for oviposition, as shown by both Smith and Maan, is the month of June, when the temperature is generally higher than in the first half of May, when oviposition by cabbage root flies takes place.

Emergence of first-generation flies.

Smith (*op. cit.*) gave 8th July as the date of emergence of first-generation flies, and Maan (*op. cit.*) gave from 3rd July–2nd August, with a peak emergence period from 8th–20th July. At Wye in 1953, first-generation flies emerged from 6th July–7th August, about 90 per cent. emerging from 6th–22nd July. In 1954, the emergence period was from 12th July–16th August, over 80 per cent. emerging during the week 18th–25th July. The time of emergence at Wye in 1953 corresponded with that recorded by Smith and by Maan; that at Wye in 1954 was a week later, probably because of the low temperatures which prevailed in 1954.

Diapause in first-generation pupae.

In 1953, 369 healthy first-generation pupae were kept under observation. Only 141 (approximately 40 per cent.) gave rise to first-generation flies during the summer. The remaining 228 pupae continued in a state of diapause.

Occasional flies emerged in late September, October and November, a matter of no significance in the life of the species, as will be shown later; but 196 pupae remained in a diapause throughout the summer, autumn and winter and gave rise to flies in April and May 1954. It was recognised that this high proportion of first-generation pupae with a prolonged diapause might be abnormal, for the flies that produced them were derived mainly from pupae with a prolonged diapause.

In 1954 flies derived from overwintered first- and second-generation pupae of the 1953 cultures, and termed univoltine and bivoltine flies, were kept separate. The two groups of flies had a similar emergence period in spring and laid eggs at the same time. Pupae were collected from both cultures at the beginning of July 1954, differences in the numbers of pupae collected being caused by errors of management of the cultures. Of 119 first-generation pupae from the univoltine flies of 1953, 27 were discarded in mid-September as dead, 91 were healthy and in a state of diapause, and one (approximately 1 per cent.) had produced a fly (on 14th July). Of 345 first-generation pupae from the bivoltine flies of 1953, 52 were discarded in mid-September as dead, 285 were healthy and in diapause and eight (approximately 3 per cent.) had produced flies (from 12th–18th July). The low emergence of first-generation flies in both groups suggested that the number of generations a year was not an inherited character; and the simultaneous occurrence of the unusually cool weather of June and July 1954 and the marked increase in the proportion of first-generation pupae with a prolonged diapause, suggested that the incidence of diapause was related to the temperature during the developmental period of the larvae. This was supported by evidence from wild larvae received from Wiltshire on 25th June 1954 and allowed to continue their development. About 425 first-generation pupae were obtained; 191 flies emerged from 16th July to 6th August, and when the remaining pupae were examined in mid-September some were dead but 182, or 49 per cent., were found to be in a state of diapause. This was a much higher proportion than that (20 per cent.) observed in 1952, when the weather during the development of first-generation larvae was much hotter than in 1954.

Second and third generations.

Smith (1922) calculated that the date for the emergence of second-generation flies would be 24th August. Maan (1945) gave no date of emergence, but stated that only a small number of second-generation flies emerged in about three weeks after causing damage in the latter part of August. At Wye in 1953, 244 second-generation pupae were kept under observation. Only two gave rise to flies in 1953, on 3rd and 24th September respectively, which was much later than the date calculated by Smith. In 1954, second-generation pupae were formed in August, but no flies had emerged by the end of September.

The observations at Wye showed that the numbers of second-generation onion flies were so small as to be negligible. Because high temperature (estimated as an air temperature of 70°F. in the field) is essential for activity and reproduction, it seems unlikely that in autumn there is any attack by third-generation larvae.

Overlapping of generations.

Both Smith and Maan recorded the overlapping of successive generations but did not define its extent and importance. At Wye, in 1953, there was no overlapping of the first and second generations in the breeding cages, the last of the spring flies having died about the time the earliest of the first-generation flies emerged. In 1954, low temperatures prevailed during June, July and August, and flies from overwintered pupae were alive and laying some eggs at the beginning of September. First-generation flies from the wild and laboratory stocks were also alive and breeding at a low rate. All onion flies in captivity were destroyed in early September, though there was no doubt that many would have remained alive and laid small numbers of eggs for some time longer.

The extent to which the generations overlap seems to depend on weather conditions. Hot, dry weather shortens the lives of the flies and tends to prevent the overlapping of the generations, and cool, moist weather has the opposite effect. The effect of overlapping of generations on the numbers of onion flies in the field and their potentiality for injury to susceptible crops is probably negligible, but this can only be determined by field studies.

Discussion.

This laboratory study of onion flies suggests that there is need for field observations on the annual cycle of generations. It would appear that there is normally one complete generation and a partial second, and that the numerical strength of the second generation is determined mainly by the temperature conditions during the larval life of the first generation. Low temperatures in June seem to affect the rate of larval development and result in pupal diapause, which may continue from late June to the following May. Warm weather in late summer and in autumn causes some of the first-generation flies to emerge from late September to November, a period when the temperature is too low to permit normal activity.

In onion flies the minimum temperature for full activity is high, as might be expected in insects that do not emerge until the beginning of summer. Laboratory observations suggest that in captivity a temperature of about 80°F. is necessary to stimulate egg-laying. In the field, where the flies are able to bask in direct sunlight, screened thermometers give an artificial measure of the temperature of the habitat, and it is probable that the threshold temperature for oviposition thus recorded would seem lower, probably 70°F. The need for relatively high temperatures to stimulate activity in the flies makes it unlikely that those emerging in late summer and autumn contribute to late attacks on susceptible crops.

Cabbage Root Fly (*Erioischia brassicae* (Bch.)).

The annual cycle of generations in the cabbage root fly was determined by Smith (1927). He found that flies emerged from overwintered pupae in May; first-generation flies emerged from late June to early September, and second-generation flies emerged from late July to mid-September.

Smith first observed egg-laying in north-west England on 31st May. This is four weeks later than the latest date (2nd May) observed by Miles (1951) in the course of six years' observations in Kent. Since oviposition in the field does not begin until the air temperature reaches 60°F. (Miles, 1954), local variations in the time for the beginning of oviposition may be expected, but it seems likely that the late finding of eggs was an error of observation, because the date given for the emergence of first-generation flies was from 29th June onwards. Even under favourable conditions the development of the first generation from egg to adult was unlikely to be completed in four weeks. Miles' observations in Kent have shown that in the period from 1948–1953 the beginning of oviposition varied from 14th April to 2nd May and was associated with a temperature of at least 60°F.

Smith (*op. cit.*) found that the peak emergence period for first-generation flies was 8th–18th July. If allowance is made for seasonal differences, this agrees with Miles' observations on the second period of egg-laying, which occurred from 28th June–14th July 1952 and from 1st–20th July 1953. Similarly, Smith recorded that the period of maximum emergence of second-generation flies was from 7th–13th August, and in 1953 Miles found that a third peak of egg-laying occurred from 5th–11th August. This general agreement between the times of emergence of flies in Lancashire and the times of egg-laying in Kent suggests that local differences in climate have relatively little effect on the times at which the several generations of *E. brassicae* are active.

Miles has shown (1954) that the annual cycle of *E. brassicae*, as indicated by numbers of eggs on host-plants, has three progressively diminishing peaks of activity. This was not the result of prolonged diapause in the first generation. On 4th–13th August 1953, 199 wild first-generation pupae were examined; 196 had already given rise to flies, two showed by the darkening eye-spots that flies would soon emerge and only one pupa (0·5 per cent.) appeared to have entered the overwintering diapause. Similarly in 1954, 374 first-generation larvae and pupae were collected from 20th–24th June; of these, 24 died, 162 were parasitised (almost entirely by Hymenoptera†), 185 gave rise to flies, and only three pupae (1·6 per cent.) entered the overwintering diapause. These data showed that there was virtually complete emergence of first-generation pupae. Smith (1927) observed that some second-generation pupae overwintered. Owing to few eggs being laid on the observation plot in July 1954, a total of only 40 second-generation pupae was obtained from 24 plants. Of these, 12 were parasitised, 23 gave rise to flies and five (18 per cent.) entered diapause, thus confirming Smith's findings. Egg-counts in three years have shown that although weather favourable to activity occurs in late summer, the number of eggs laid is small; and consequently there is little likelihood of high populations of larvae in late summer and autumn.

An understanding of the annual cycle of generations and the extent of activity associated with each is of value in interpreting field conditions. In a study of root maggots on turnips in Ontario (Oughton, 1952), the numbers of larvae of *E. brassicae* on four crops from June to October were shown graphically. From knowledge of the annual cycle of *E. brassicae*, it seems probable that only two of the fields were infested with more or less pure cultures of *E. brassicae*; the sudden great rises in the larval populations of the other two fields in August and September appears to be caused by the intrusion of an autumn-feeding species, probably *E. floralis* Fall., whose presence could have been determined had the differences in the annual pattern of activity of the two species been known and recognised.

Turnip Root Fly (*Erioischia floralis* (Fall.)).

The turnip root fly, *E. floralis* (Fall.), has not been found in England, but it occurs in Scotland (Morison, 1937) and it is distributed widely over northern regions of Europe, Asia and America. Its host range appears similar to that of *E. brassicae* but it is mainly associated with attacks on turnips and swedes. Through the kind help of Dr. Guy Morison of Marischal College, Aberdeen, the writer has had *E. floralis* for observation. Starting with pupae transferred from north Scotland to Kent during the winter of 1949–50, the species was maintained for three seasons, and cultures started with pupae transferred in the winter of 1952–53 are still in being.

The annual cycle of generations of *E. floralis* differs greatly from that of *E. brassicae*. Observations in Denmark from 1931–1952 (Wagn, 1953) showed that flies emerged from overwintered pupae from late June to the end of September, and in 1952 a representative sample showed a peak emergence period in the second week of August. In Scotland, *E. floralis* emerged from June to the end of August, with a peak emergence period in the first week of August (Morison, *op. cit.*). In Kent, for five seasons, *E. floralis* emerged from overwintering pupae from late June to mid-September, as in more northerly regions, but the peak emergence period was the third or fourth week of July, 1–2 weeks earlier than in Denmark and Scotland. It is evident that emergence from mid- to late summer is characteristic of *E. floralis*, and that the change in climate associated with the transfer from north-east Scotland to south-east England (approximately 6° latitude or 400 miles) did not modify the time of emergence of the flies to any marked extent.

---

† Identified by G. J. Kerrich as *Trybliographa rapae* (Westw.).

In Denmark and Scotland it has been recognised that *E. floralis* is univoltine and that the larvae are present on the host-plants from August to October, populations of 50–70 pupae per turnip being frequent (Morison, *op. cit.*). In Kent, the flies laid eggs freely in the cages in July and August and pupae were present in the cultures from August onwards. First-generation flies emerged from the beginning of September, throughout October and occasionally in November. For three seasons, flies emerging in September were kept in breeding cages under conditions similar to those in which the overwintered flies were successfully maintained, but no eggs were obtained, probably because the temperatures were too low to stimulate egg-laying. Flies from overwintered pupae are active during a period of declining temperature and the threshold for oviposition cannot be determined without artificially controlled temperatures, which were not available to the writer.

From the behaviour of *E. floralis* in captivity, it was possible to observe some of the means by which climate regulates the distribution of insects. The transfer of the species from Scotland to Kent appeared to bring forward the period of maximum emergence from the first half of August to the latter half of July. As a result of the early emergence of the adults of *E. floralis*, their larvae developed at high temperatures and therefore rapidly, and the pupae, instead of entering the overwintering diapause, gave rise to first-generation flies. By the time these emerged, the temperature was too low for normal activity and they died without laying eggs. These observations on *E. floralis* confirmed the suggestions of Mellanby (1939) that the geographical range of an insect species is limited less by the upper and lower lethal temperatures than by the narrow temperature zone in which normal activity takes place, and that the greatest single factor controlling distribution is probably the temperature below which full activity does not occur. At Wye, the temperature in September does not rise sufficiently often above the minimum at which *E. floralis* is fully active, and consequently, although all other factors are favourable, the species does not survive in capitivity. In order to maintain laboratory cultures, it has been necessary to keep first-generation pupae at an artificially low temperature and thus prevent the emergence of flies in the autumn.

Bean Seed Flies (*Delia cilicrura* (Rond.) and *D. trichodactyla* (Rond.)).

The annual cycle of generations of the bean seed flies, and their relative numbers and importance at various times of the year have not yet been fully investigated. The larvae are scavengers in the soil and feed on organic matter, crop residues and the roots and underground stems of plants, and occasionally they live as predators on other insects. Their unspecialised feeding habits distinguish larvae of the bean seed flies from those of the several preceding species and make it difficult to forecast their attacks on crops. The flies are attracted to the soil by cultural operations such as ploughing, hoeing and harrowing and they lay eggs under clods and in soil crevices. At other times they shelter in the vegetation of cultivated ground, headlands and hedgerows, where they also lay eggs. They seem to prefer sheltered positions for oviposition when these are readily available, and on several occasions the writer obtained the eggs under artificial plants, which consisted of short canes to which pieces of brown paper had been tied before they were inserted in the soil.

No means of measuring the activity of the bean seed flies throughout the year has yet been devised. Like cabbage root flies, they suddenly appear in large numbers in the latter part of April and in May. The ease with which they can be attracted to soil on warm spring days suggests that their activity is affected by the temperature, and their occurrence in large numbers at the time when cabbage root flies are active seems to indicate that the two species have the same threshold temperature for full activity, that is, approximately 60°F. on screened thermometers in the field. Little is known of the field conditions under which egg-laying by bean seed flies takes place because the short incubation period makes it difficult to study the intensity of egg-laying and the distribution of eggs. Differences in the host range of the larvae under different crop sequences and at different times of the year make it difficult to observe the annual cycle of generations.

Miles (1948) reconstructed the annual cycle of generations from field observations in the west of England, and further observations in Kent have confirmed that there are four generations a year. The attacks of first-generation larvae on germinating beans in May and June and the emergence of first-generation (called "second generation" in 1948) flies in June–July are well known. Miles (*op. cit.*) showed that second-generation larvae fed on leeks, but other seeds and plants set out when the first-generation flies are active are also liable to be attacked. At Wye, in 1949, third-generation larvae completely destroyed germinating beans in early August, and since then attack on beans sown in frames during the first half of August has been noted on several occasions. The large numbers of adults present in late September and early October, and the finding of larvae on spring cabbages and lettuce set out at that time, give evidence of the occurrence of a fourth generation.

The factor that limits the activity of bean seed flies in Britain appears to be the temperature. Ristich * (Cornell University, Ithaca, N.Y.) was able to rear *D. cilicrura* continuously for twelve generations in a greenhouse, and in North Carolina (U.S.A.) it appears to breed out-of-doors all the year round (Reid, 1940). It seems likely that the outdoor temperature below which egg-laying does not take place is about 60°F., and in England there are few sustained periods with temperatures above this level after mid-October. The long period of activity in the bean seed flies and their large numbers in late autumn seem to be associated with their feeding habits; being scavengers and general feeders, their annual cycle of activity has not been restricted and modified by interaction with the life-cycle of a host-plant.

Conclusions.

These biological studies of root-infesting Anthomyiid flies have shown that although the species are closely related and similar in many of their habits, their life-cycles are distinct and their normal activity governed by different temperatures. They have also shown that from the point of view of agriculture and horticulture the biological unit for investigations on insects should be the annual cycle of the species in its habitat and not merely the life-cycle of the individual, because conclusions gathered from the study of one generation are not necessarily applicable to subsequent generations which develop at different seasons. They have further shown the need for more exact knowledge of the economic importance of injurious insects at different times of the year, since it appears that under field conditions such factors as the biotic potential may be severely restricted by the direct and indirect effects of climate on the length of adult life.

---

* In correspondence.

Summary.

Field and laboratory studies have shown that the several root-infesting Anthomyiid flies differ greatly in the number of generations composing their annual cycle and in the minimum temperature conditions necessary for full activity.

Onion flies (*Delia antiqua* (Mg.)) were mainly univoltine in laboratory cultures. Of 369 first-generation pupae studied in 1953, only 141 (about 40 per cent.) gave rise to flies in July–August and 228 (about 60 per cent.) entered a diapause, in which 196 (about 85 per cent. of those entering diapause) remained until the following spring. In 1954, 99 per cent. of the first-generation pupae from univoltine flies and 97 per cent. of those from bivoltine flies entered the overwintering diapause in July. It then appeared that exposure to low temperatures during the development of the first-generation larvae had induced diapause in the pupae. This was confirmed by the unexpectedly high proportion (49 per cent.) of wild first-generation pupae which entered the overwintering diapause in July in the cool summer of 1954. It was also established that the spring oviposition period for *D. antiqua* began about the end of May, and it appeared that, in the field, air temperatures of approximately 70°F. were necessary to stimulate egg-laying. First-generation flies emerged in the second and third weeks of July, their numbers depending on the temperature in June. A few second-generation flies, together with late first-generation flies, may emerge in September, but the temperature is then too low for oviposition and there seem to be no third-generation larvae.

The annual cycle in the cabbage root fly (*Erioischia brassicae* (Bch.)) comprised two generations and a partial third. Oviposition usually began in the latter part of April and was associated with an air temperature of at least 60°F. There was virtually complete emergence of flies from first-generation pupae, counts in 1953 and 1954 showing that only 0·5 and 1·6 per cent., respectively, entered the overwintering diapause. Highest numbers of flies occurred in the first half of July, but summer weather adversely affected their survival and they laid relatively small numbers of eggs. An incomplete second generation emerged in the first half of August and although weather conditions appeared favourable, few eggs were laid. Overwintering pupae were derived from eggs laid by flies of the first and second generations.

The turnip root fly (*E. floralis* (Fall.)) was transferred in the pupal stage in winter from Ross (northern Scotland) to Kent (south-eastern England) without affecting the period during which the emergence of flies occurred, but the time of maximum emergence appeared to be advanced from the first half of August to the second half of July. First-generation larvae normally feed in late summer and early autumn and there appears to be only one generation a year. The higher temperatures of Kent increased the rate of larval and pupal development and led to the emergence of adults in September, when the temperatures were too low for oviposition.

The development of successive generations of the bean seed flies (*D. cilicrura* (Rond.) and *D. trichodactyla* (Rond.)) appears to be limited only by temperature conditions, a minimum air temperature of 60°F. in the field being required to stimulate oviposition. There is reliable evidence that in England there are four generations a year and high populations of third-generation adults occur in late September and early October.

Acknowledgements.

The writer thanks the Principal and Governors of Wye College for facilities for the work and the Royal Society for a grant for insect cages and other apparatus. She gratefully acknowledges the criticism and help given by Professor Herbert W. Miles in whose department the work was done. She also thanks Mr. G. Barnes, National Agricultural Advisory Service, Trowbridge, Wilts., for providing onion-fly larvae for these studies, and Miss B. Cooper for assistance with the tedious work of separating puparia from soil.

References.

MAAN, W. J. (1945). Biologie en phaenologie van de uienflieg, *Chortophila antiqua* (Meigen) en de preimot, *Acrolepia assectella* (Zeller), als grondslag voor de bestrijding.—Meded. TuinbVoorlichtingsdienst, no. 39, 92 pp.

MELLANBY, K. (1939). Low temperature and insect activity.— Proc. roy. Soc., (B) **127,** pp. 473–487.

MILES, M. (1948). Field observations on the Bean Seed Fly (Seed Corn Maggot), *Chortophila cilicrura*, Rond., and *C. trichodactyla*, Rond.—Bull. ent. Res., **38,** pp. 559–574.

MILES, M. (1951). Factors affecting the behaviour and activity of the Cabbage Root Fly (*Erioischia brassicae* Bché).—Ann. appl. Biol., **38,** pp. 425–432.

MILES, M. (1953*a*). Studies of British Anthomyiid flies . . . V. The Onion Fly, *Delia antiqua* (Mg.).—Bull. ent. Res., **44,** pp. 583–588.

MILES, M. (1953*b*). Field studies on the influence of weather conditions on egg-laying by the Cabbage Root Fly, *Erioischia brassicae* Bché. I.—Ann. appl. Biol., **40,** pp. 717–725.

MILES, M. (1954). Field studies on the influence of weather on egg-laying by the Cabbage Root Fly, *Erioischia brassicae* Bché. II.—Ann. appl. Biol., **41,** pp. 586–590.

MORISON, G. D. (1937). Turnip Root Fly problem.—Aberdeen Pr. & J., January 21, 1937.

OUGHTON, J. (1952). A study of turnip root maggots in Ontario.—82nd Rep. ent. Soc. Ont. 1951, pp. 77–84.

REID jr., W. J. (1940). Biology of the Seed-corn Maggot in the coastal plain of the South Atlantic States.—Tech. Bull. U.S. Dep. Agric., no. 723, 43 pp.

SMITH, K. M. (1922). A study of the life-history of the Onion Fly (*Hylemyia antiqua*, Meigen).—Ann. appl. Biol., **9,** pp. 177–183.

SMITH, K. M. (1927). A study of *Hylemyia* (*Chortophila*) *brassicae* Bouché, the Cabbage Root Fly and its parasites . . .—Ann. appl. Biol., **14,** pp. 312–330.

WAGN, O. (1953). Om den store kålflue (*Chortophila floralis* Fall.).—Tidsskr. Planteavl, **56,** pp. 470–477; also as Beretn. Forsøgsv. PlKult., no. 470.

STUDIES OF BRITISH ANTHOMYIID FLIES.

VII.—THE ONION-FLY COMPLEX.

By Mary Miles
Wye College (University of London).

The onion fly, *Delia antiqua* (Mg.), is considered to be the most serious pest of onions in private and market gardens throughout Britain. According to Wilson (in Chittenden, 1951), "it is most destructive in spring and early summer when the plants are young". A study of the biology of *D. antiqua* has shown, however, that its activity is limited to the period about mid-summer. Smith (1922) found that eggs were first laid in late May and early June, and Wright (1939) confirmed this by observing that, on 1st June, eggs and very small larvae were present on his experimental plots. It seems generally known that insect damage to onions occurs earlier than June; it appears, therefore, that some other species is involved in the attacks. Both Smith and Wright were concerned with damage to field crops, but neither recorded having reared flies from representative samples of larvae to ascertain whether any species other than *D. antiqua* was present.

Ormerod (1883) first drew attention to the fact that two species of Anthomyiid flies were concerned in the attacks on onions. In 1882, she submitted specimens of larvae infesting onions from different parts of Britain to Meade, an English authority on Diptera, who bred from them not only *D. antiqua* but also *Anthomyia platura* Mg., now recognised as synonymous with *D. cilicrura* (Rond.) (Séguy, 1923), a species then known in Europe as the shallot fly. Ormerod tried to distinguish the two species by their habits, and associated *D. antiqua* with eggs laid on the foliage of onions and *D. cilicrura* with eggs laid either at the sides or bases of the bulbs. She later found that larvae of both species fed at the base of the bulbs, but she established that both species were pests of onions. In her "Manual of Injurious Insects" (1890) she again mentioned the two species on onions, but her observations seem to have been overlooked by later entomologists.

In field studies of the bean seed flies (the common name for *D. cilicrura* and *D. trichodactyla* (Rond.)), the writer found (Miles, 1948) that *D. cilicrura* was present on onions in association with *D. antiqua*, and that second-generation larvae of *D. cilicrura* infested leeks, though these were not attacked by *D. antiqua*. Merrill (1951) and Merrill & Hutson (1953) reared Diptera from onions in Michigan and found that, although *D. antiqua* was the most numerous species throughout the season, up to one-fifth of the flies reared in May and June from attacked onions were *D. cilicrura*, and at one centre where severe infestation occurred early in the season and affected 10–50 per cent. of the seedlings in a large planting, representative samples showed that only *D. cilicrura* was present. These observations in England and America suggest that *D. cilicrura* may be a more serious and widespread pest of onions than has generally been recognised.

Life-histories of the two Species.

Comparative studies of the life-cycles of some root-infesting Anthomyiid flies (Miles, 1955) have made it possible to define with reasonable accuracy the times and circumstances of attack by *D. cilicrura* and *D. antiqua*, respectively. Larvae of *D. cilicrura* are unspecialised feeders, whose occurrence in large numbers on cultivated land is associated with the mechanical disturbance of the soil at times when the flies are active. In England, adults of *D. cilicrura* may be found from April to mid-October, and there appear to be four generations a year, with peaks of egg-laying in late April to mid-May, late June to mid-July, in the first half of August, and mid-September to early October. The incubation period is short, and injury to crops by the larvae can usually be detected about the times that the several peak periods of oviposition come to an end.

Larvae of *D. antiqua* are specialised feeders on *Allium* spp. and their presence on onions is due to the chemotropic responses of the adults to the crop. Flies of *D. antiqua* are active from the end of May to the beginning of August, and in England there is one complete generation a year with a partial second (Miles, 1955). The peak period of egg-laying for the overwintering generation is from late May to about the middle of June, and the first-generation flies lay eggs mainly from the middle to the end of July. Ormerod (1878–85) gave a comprehensive series of records of the occurrence of *D. antiqua* in many parts of England and Scotland, and of eleven dated occurrences, nine refer to attacks in the period from late May to July. Later (Ormerod, 1893) she quoted from John Curtis that "June and July are the months in which they [larvae of onion fly] are in full force"; this is the period when first-generation and early second-generation larvae are feeding.

Cultivation of Onions in relation to Attack.

In order to appreciate fully the differences in the times and circumstances of attack on onions by *D. cilicrura* and *D. antiqua*, it is necessary to review the cultivation of onions in relation to the activity of the flies. Onion seed is sown in suitable weather on or after the traditional date, 14th February (Anon., 1949), and germination takes about three weeks. As soon as the rows of seedlings are visible the work of weeding starts; the first hoeing is usually done in April and hoeing and weeding continue to the middle of July. Any disturbance of the soil attracts adults of *D. cilicrura.* The gravid females assemble on the freshly broken surface and lay eggs under small clods and dying weeds, in the shelter of leaves, and in crevices in the soil near the plants. Onion seed is usually sown before flies of *D. cilicrura* emerge from overwintering pupae, but in the period from April to the middle of July, when the seedlings are hoed and weeded, there are two peak periods of activity of *cilicrura.* There seems no doubt that the occurrence of larvae of *D. cilicrura* in seedling onions is associated with weeding and hoeing. Ormerod (1881) recorded from Falkirkshire that the tips of the leaves of onions turned yellow at the beginning of May, and that when damaged plants were pulled up they were found to be full of maggots. Since onion-fly larvae do not occur in Britain at this early date, it is practically certain that the species concerned in this attack was *D. cilicrura*, especially as the immediate removal of infested plants resulted in "as fine a crop of onions as could be desired", an observation that indicated that *D. antiqua* was not present in the crop later in the season.

In June and July, when attack by larvae of *D. antiqua* takes place, onion plants are usually well developed, and the characteristic sign of attack is the presence in the crop of rotting bulbs, often infested by 20–30 maggots (Chittenden, 1951). It is this form of attack that is best known to growers and is correctly ascribed to onion fly. Onions are usually harvested in September, but in suitable weather they may be left in the field for a much longer period (Anon., 1949). From June onwards until the onions are finally removed to store some larvae and flies of *D. antiqua* may be found about infested crops, but after the end of July the activity of the species rapidly declines, and late larvae and flies are of little importance. The dispersal of onion flies is limited by the long life of the crop on one site and the simple pattern of cropping (compared with the complicated annual pattern of cropping with Brassicas).

A modified form of onion cultivation is frequently adopted. Seed is sown in the second week of August, and the plants are overwintered in the seed beds and set out in their permanent sites in March (Smith, 1954). It was claimed (Roebuck, 1922) that the use of transplanted seedlings was advantageous as a means of avoiding attack by onion fly, but it is difficult to see why, because exposure to attack does not take place until approximately two months after transplanting. Consideration of Roebuck's data suggests that *D. antiqua* was not present in any of his crops, and that it has not yet been shown that changing the method of cultivating onions affects the intensity of attack by *D. antiqua*.

Injury by Anthomyiid larvae to the germinating seeds of onions sown in August has frequently been observed, and the attacks are ascribed to *D. antiqua*. Activity by *D. antiqua* is negligible at this time of the year and it is improbable that the ageing flies leave the mature crops on which they are established for germinating seedlings. Larvae on seedling onions in August have been identified as *D. cilicrura* (Miles, 1953), and it is likely that attack by this species is widespread because the preparation of the seed beds in early August coincides with the peak period of activity of the second-generation flies.

Effect on Control Measures.

The recognition that onions are subject to a complex pattern of attack by dipterous larvae whose times of attack can be forecast makes a reconsideration of control measures against onion fly necessary. In 1936 to 1938 a series of experiments on the control of onion fly (*D. antiqua*) by chemical means was carried out at Cambridge (Wright, 1938, 1939) and for over fifteen years the results of these trials have provided the basis for recommendations to growers. For this reason they are considered in detail here.

Re-interpretation of the results of the Cambridge experiments is hampered by some inconsistencies with regard to the life-history of the onion fly, by the fact that the onion crops concerned were not in the normal stage of growth for the time of the year, and by the lack of any assessment of intensity of attack in entomological terms. It was stated (Wright, 1938) that the life-cycle of *D. antiqua* in the eastern counties was substantially similar to that recorded by Smith (1922). yet, in the 1937 experiments, insecticidal treatment, *e.g.*, the application of corrosive sublimate solution, was made twice (on 15th and 25th May) before the date (28th May) given by Smith for egg-laying; further, the first-generation flies in 1938 were recorded as beginning to emerge by the last week of June, two weeks earlier than the date (8th July) given by Smith, and only three weeks after 1st June, when examination of the plants had revealed " that onion fly eggs were present in the soil near the plants, and that a small percentage had hatched, and very small larvae were found " (Wright, 1939).

The dates at which onions were sown in the Cambridge experiments were 22nd April (1937) and 3rd May (1938), approximately two months later than the usual time. This greatly influenced the effectiveness of the calomel (mercurous chloride) seed-dressing ($\frac{1}{2}$–1 lb. of 4 per cent. calomel dust per 1 lb. onion seed) for the control of onion fly. Onion seed is usually sown at a depth of about a quarter-of-an-inch in the soil. Egg-laying by onion flies occurred about a month after sowing on the experimental plots, while the seedlings were still in the " needle " or " loop " stage; and it is obvious that at this time the concentration of mercury vapour, an ovicide (Wright, 1940), was sufficiently high to kill eggs laid on or near the seedlings. Under usual conditions of cultivation, onion seed is sown about three months before egg-laying by *D. antiqua*, and it is doubtful whether after so long a time, the concentration of mercury vapour from seed treated with calomel would be sufficiently high to be toxic to eggs of this species, especially as the normal growth of the plants would result in the eggs being deposited much further away from the source of the vapour, namely, the old seed-coat.

The application of 4 per cent. calomel dust to the seedlings (1 lb. per 50 row-yards) also gave satisfactory control of onion fly at Cambridge in 1938. This treatment should give similar results under usual cropping conditions provided that the time of application is related to the time of attack by onion fly and not, as Wright (1939) recommended, " after germination ". In the Cambridge experiments the seed was sown abnormally late and consequently the seedlings were only at the " loop " stage of development when attack took place; but under usual cropping conditions the " loop " stage of the seedlings occurs about two months before egg-laying by onion flies, and it is doubtful whether calomel dust applied at that time would retain its ovicidal properties long enough to give satisfactory results. A suitable time for applying calomel to protect onions against attack by *D. antiqua* is the beginning of the fourth week of May, and one application at that time should give adequate protection. What is questionable, however, is whether a poison such as mercurous chloride is suitable for use on onions at a time when they are nearly large enough for bunching and marketing.

The assessment of results of the various experiments in terms of numbers of plants and weight of crop, supported by statistical analyses, obscures the fact that the onion fly, *D. antiqua*, was probably absent from some of the series of trials. There is no evidence of the presence of onion flies on the series of randomised plots laid out at Cambridge in July 1937 (Wright, 1938), and the biology and habits of the species virtually preclude its occurrence in onion beds sown at this abnormal time. Further, it appears probable that larvae of onion fly were not present on the plants in the series of trials in four school gardens in 1938 (Wright, 1939). The absence of the onion flies from onion plantings is not surprising, for their distribution is erratic and there are districts where onions and leeks have been grown regularly for long periods without any attack by *D. antiqua*. In these circumstances the omission of data on infestation from the accounts of experiments designed to control *D. antiqua* raises the question of the validity of some of the conclusions.

Discussion.

This review of the " onion-fly " problem has shown that more field observations are necessary to determine the distribution of *D. antiqua* and to assess the importance of *D. cilicrura* as a pest of onions. *D. cilicrura* is generally distributed and numerous, and is an obscure but persistent pest of a wide range of crops. *D. antiqua*, on the other hand, has a limited distribution, probably because the area devoted to onion crops has always been relatively small (in comparison, for example, with the area given annually to Brassicas), their special requirements have led to their intensive cultivation in only a few districts, often on the same sites for several seasons, and their long period of growth has eliminated the need for any dispersal of the first-generation flies. Larvae of *D. antiqua* and *D. cilicrura* resemble each other closely, but they can be distinguished by the number of processes of the anterior spiracles, larvae of *D. cilicrura* having 5–8 processes and larvae of *D. antiqua* having 10–13 processes.

Differences in the times and habits of the two species suggest that measures to check their attacks may need separate consideration. The activity of the onion fly, *D. antiqua*, is restricted by its temperature requirements to the period from the end of May to about the end of July, a time when onions are well developed. The bean seed fly, *D. cilicrura*, reaches full activity at a lower temperature and appears to be most injurious to spring-sown onions in May and to summer sowings in August. It seems possible that the widespread use of chemical weed-killers in onion beds may limit the spring attack on seedlings by *D. cilicrura*, for when chemicals are used there is little disturbance of the soil to attract the flies to the seed beds; but this needs investigation. Conditions are totally different for onions sown in August, for the soil may become infested by *D. cilicrura* during the preparation of the seed bed. The use of the calomel seed-dressing is not likely to give effective control of *D. cilicrura*, because the eggs are not necessarily laid in proximity to the seeds, but through its fungicidal properties it may increase the survival rate of the seedlings so that the crop can better withstand attack.

The confusion and difficulty with regard to the species of Anthomyiid flies concerned in attacks on onions have also shown the need for exact observations of the time and intensity of insect attacks, for precise determination of the species concerned in injury at different seasons, and for the use of entomological standards when assessing infestation of crops and the results of control measures.

Summary.

Onions are attacked by larvae of Anthomyiid flies from May to August. Two species are concerned, namely the onion fly, *Delia antiqua* (Mg.), and the bean seed fly, *D. cilicrura* (Rond.). The onion fly, which in some seasons is mainly univoltine, attacks the crop in June and July. The bean seed fly, which has 3–4 generations a year, is most injurious to spring-sown onions in May and to summer-sown onions in August. Attack by *D. antiqua* is the result of the chemotropic response of the species to its host-plants. Attack by *D. cilicrura* follows the disturbance of the soil during cultural operations in April–May, and occurs again when seed-beds are prepared for August sowings.

The recognition of this complex pattern of attack makes it necessary to reconsider the value of established control measures. The calomel (mercurous chloride) seed-dressing is unlikely to give control of onion fly because its ovicidal efficiency is impaired by exposure to the air during the three months between the sowing of onion seed (end of February) and oviposition (end of May), and by the growth of the plants, which results in the eggs being laid at some distance from the old seed-coat which carries the ovicide. It is also unlikely to have a direct effect on infestation by bean seed fly, because the eggs of this species are not necessarily laid on the seedlings and, in the case of August sowings, the eggs may have hatched before the seed is sown.

Acknowledgements.

The writer thanks the Principal and Governors of Wye College for facilities for this investigation. She also gratefully acknowledges the continued help of Professor Herbert W. Miles.

References.

Anon. (1949). Onions and related crops.—Bull. Minist. Agric., no. 69, 3rd edn.

Chittenden, F. J. (1951). Dictionary of gardening.—4 vols. London, Oxford Univ. Press.

Merrill jr., L. G. (1951). Diptera reared from Michigan onions growing from seed.—J. econ. Ent., **44,** p. 1015.

Merrill jr., L. G. & Hutson, R. (1953). Maggots attacking Michigan onions.—J. econ. Ent., **46,** pp. 678–680.

Miles, M. (1948). Field observations on the Bean Seed Fly (Seed Corn Maggot), *Chortophila cilicrura*, Rond., and *C. trichodactyla*, Rond.—Bull. ent. Res., **38,** pp. 559–674.

Miles, M. (1953). Studies of British Anthomyiid Flies. . . . V. The Onion Fly, *Delia antiqua* (Mg.).—Bull. ent. Res., **44**, pp. 583–588.

Miles, M. (1955). Studies of British Anthomyiid Flies. VI. The annual cycle of generations in some Anthomyiid root flies.—Bull. ent. Res., **46**, pp. 11–19.

Ormerod, E. A. (1878–85). Notes (Reports) of observations of injurious insects, 1877–84. London.

Ormerod, E. A. (1890). A manual of injurious insects. . . .—2nd edn., 410 pp. London, Simpkin, Marshall.

Ormerod, E. A. (1893). Report of observations of injurious insects, 1892. London.

Roebuck, A. (1922). Experiments on cultural methods of controlling Onion Fly (*Hylemyia antiqua*, Meigen = *Phorbia cepetorum*, Meade).—Bull. Chamb. Hort., **1**, pp. 8–10.

Séguy, E. (1923). Faune de France. 6. Diptères Anthomyides, p. 122.—Paris, Lechevalier.

Smith, T. (1954). Profitable culture of vegetables, Revised by J. Rhodes.—3rd edn., p. 201. London, Longmans Green.

Smith, K. M. (1922). A study of the life-history of the Onion Fly (*Hylemyia antiqua*, Meigen).—Ann. appl. Biol., **9**, pp. 177–183.

Wright, D. W. (1938). The control of the Onion Fly.—J. Minist. Agric., **44**, pp. 1081–1087.

Wright, D. W. (1939). The control of Onion Fly (*Delia* (*Hylemyia*) *antiqua* Meig.).—J. Minist. Agric., **46**, pp. 147–154.

Wright, D. W. (1940). The control of the Cabbage Root Fly.—J. Minist. Agric., **46**, pp. 765–772.

A COMPARISON OF A GROUP OF GALL MIDGES OF THE GENUS *THOMASINIANA* STRAND, E. 1916 AND A DESCRIPTION OF A NEW SPECIES FROM WILD BLACKBERRY.*

By R. S. Pitcher
East Malling Research Station.

The writer's attention was first directed to the genus *Thomasiniana* at a time when it contained only three described species, namely, *T. oculiperda* (Rübs.), *T. theobaldi* Barnes, *T. crataegi* Barnes and one, as yet undescribed, from *Ribes alpinum* (Barnes, 1944). Since then, *T. salvadorae* has been described by Rao (1951), *T.* (*Clinodiplosis*) *oleisuga* (Targ.) has been placed in this genus by Goidanich (Grandi, 1951) and *T. lavandulae* described by Barnes (1953*b*). With the exception of *T. salvadorae*, all species feed under the surface tissues of their host-plant but do not form galls.

This paper confines its comparison to the species with Rosaceous host-plants, namely the first three to be described, and another, hitherto undescribed, from wild blackberry. It is an extremely difficult group to separate on morphological grounds, but a clear distinction can be made on the basis of the preferred host-plant. *T. oculiperda* (the Red Bud Borer) has been known since 1881 as a pest of newly budded rose and fruit-tree rootstocks, which its larvae damage by feeding on the cambial layers of stock and scion (Barnes, 1931). The writer has also found large colonies of larvae in broken branches of established apple trees and in man-made wounds on hedgerow roses. *T. theobaldi* (the Raspberry Cane Midge) is a pest of raspberries; its larvae feed between the epidermis and periderm and in so doing render the cane liable to attack by fungal pathogens (Pitcher & Webb, 1952). *T. crataegi* (the Hawthorn Stem Midge) lives on hawthorn, damaging the cambium and often causing die-back of shoots (Barnes, 1939). Larvae belonging to this genus were found on wild blackberry by Wilson, who believed them to be *T. theobaldi* (Wilson & Green, 1944). The writer has found such larvae commonly on hedgerow blackberries in south-east England but has been able to demonstrate several points of difference between them and *T. theobaldi*.

The value of trials on host-plant preference in distinguishing between closely related midges has already been shown by Barnes (1931, 1939, 1944 and 1953*a*) and in a previous paper the writer has given an account of similar trials undertaken to determine the status of *T. theobaldi* (Pitcher, 1952). This work has now been extended and on this basis, on other smaller biological differences and on a series of comparative measurements, an attempt is now made to establish the specific relationship of all the members of this group of midges.

Trials on Host-plant Preference.

The technique used was substantially that already developed for *T. theobaldi* (Pitcher, 1952). Cut shoots of each host-plant were slit to provide equivalent oviposition sites and then exposed in a cage or insectary to free-flying midges of the form to be tested. Counts of eggs were made two to three days after first exposure, giving an estimate of the relative acceptability of each host-plant to the midges and counts of third-instar larvae were made two to three weeks later. Although midges could be bred from these mature larvae irrespective of the host-plant on which they were raised, the data so obtained are not presented as they are subject to the influence of additional factors quite unrelated to the suitability of the host-plant.

---

* Including some data already presented in a thesis approved for the Degree of Doctor of Philosophy in the University of London.

In the majority of the trials, apple (rootstock M.IX), wild blackberry (*Rubus fruticosus*), raspberry (Malling Enterprise), rose (*Rosa canina*), and sometimes hawthorn (*Crataegus oxyacantha*) were used as the basic test plants. The results of these trials are summarised in Tables I–V. Loganberry, blackthorn (*Prunus spinosa*) and various fruit-tree rootstocks were also included in some of the trials and the results of these supplementary tests, together with those of the main trials, are discussed in the text accompanying each Table.

To obtain the means; the figures have been transformed to log (n + 3/8), averaged and retransformed. Statistical analysis was applied to the egg figures for all host-plants except hawthorn. The larval figures, which gave a much more consistent picture than did those of eggs, were judged to be sufficiently clear as they stood.

It is not altogether surprising that oviposition tends to be at random, as there are probably three factors influencing the female midge when choosing a host-plant, namely:—

(i) selection of a landing site after flight,

TABLE I.

Trials on host-plant preference, *T. theobaldi*.

Trial No.	Date commenced	Apple	Blackberry	Raspberry	Rose	Hawthorn
		Eggs				
1	9th August, 1947 ..	45	561	574	443	20
2	21st August, 1947 ..	190	414	847	679	10
4	30th August, 1948 ..	106	358	781	196	10
5	10th September, 1948	66	190	776	215	16
	Mean	88·7	354·4	739·9	338·4	13·4
		Larvae				
3	7th August, 1947 ..	0	0	190	33	0
4	30th August, 1948 ..	0	0	290	103	0
5	10th September, 1948	0	0	606	150	0
	Mean	0	0	323·1	80·8	0

(ii) physical suitability of the slit made in the host-plant,
(iii) biochemical relationships between midge and host-plant.

It is difficult to assess the relative importance of each factor as far as oviposition is concerned but, in the case of larval feeding and growth, only factors (ii) and (iii) can operate and although factor (ii) does exert some influence, factor (iii) is clearly the dominant one. It is the larval figures, therefore, which give the truest picture of the suitability of any one host-plant for any one form of midge.

T. theobaldi clearly preferred raspberry for oviposition, but laid eggs readily on other host-plants. Of these only rose supported the larvae; the complete failure of blackberry was rather unexpected. Of many other hosts tested, only loganberry and Himalaya Giant blackberry (*R. procerus*) supported larvae, the former being the equal of raspberry. (For further figures and statistical analysis see Pitcher, 1952.)

TABLE II.

Trials on host-plant preference, *Thomasiniana* sp., from blackberry.

Trial No.	Date commenced	Apple	Blackberry	Raspberry	Rose
		Eggs			
1	19th May, 1948	0	39	0	0
2	1st June, 1949	159	144	112	194
3	10th June, 1949	4	160	32	56
6	3rd September, 1950 ..	2	221	13	5
	Mean	4·6	119·8	11·3	11·9
		Larvae			
1	19th May, 1948	0	29	0	0
2	1st June, 1949	0	119	2	0
3	10th June, 1949	0	45	1	0
4	30th May, 1948	0	150	0	0
5	24th June, 1948	0	103	0	33
6	3rd September, 1950 ..	0	319	0	3
	Mean	0	95·0	0·25	0·77

The *Thomasiniana* sp. from wild blackberry resembled *T. theobaldi* in its non-selective oviposition (there are no significant differences between host-plants), and in its ability to raise a few mature larvae on rose. On *Rubus* spp., however, it was the reverse of *theobaldi*, showing a marked preference for blackberry, on which it laid more eggs and raised many more larvae than on raspberry. Loganberry was included in two of the trials and some eggs were laid on it, but no larvae reached maturity.

In addition to the data ~~tabulated above~~, loganberry was offered in two trials in Table but no eggs were laid; cherry and pear were offered twice and eggs laid once on each; blackthorn, plum, quince and peach were offered once and eggs were laid

time.

on all except quince.) *T. oculiperda* from apple showed a significant preference for apple for oviposition but would lay eggs on many other species. The genus *Rubus* seemed to exert no consistent attraction although eggs were laid on it from time to time. Larvae survived readily on apple, occasionally on rose and, on the one occasion on which it was tested, on blackthorn.

sert "In
ddition..."
om p.29

T. oculiperda from rose, while resembling *T. oculiperda* from apple in their neglect of *Rubus* spp., showed no significant oviposition preference for rose and on two occasions (Trials 1 and 3) laid more eggs on apple than on rose. The larvae, too, were quite tolerant of apple, only once completely failing to survive. Thus, although retaining a certain preference for their original host-plant, the *T. oculiperda* from rose appeared to be more flexible than those from apple.

Table V

In addition to the data ~~tabulated above~~, blackthorn, plum and cherry were each offered once to *T. crataegi*, but no eggs were laid. Thus these trials provided no evidence that the species had any host other than hawthorn.

TABLE III.

Trials on host-plant preference, *T. oculiperda*, from apple.

Trial No.	Date commenced	Apple	Blackberry	Raspberry	Rose	Hawthorn
		Eggs				
1	1st August, 1947 ..	181	0	0	22	—
2	23rd August, 1947 ..	108	—	0	12	7
3	30th September, 1947	29	57	0	10	0
4	28th May, 1948 ..	22	0	0	1	—
5	1st June, 1948 ..	105	0	0	0	—
6	4th June, 1948 ..	128	0	7	9	—
7	30th July, 1948 ..	45	0	0	0	0
	Mean	68·8	0·48	0·19	3·0	0·62
		Larvae				
1	1st August, 1947 ..	84	0	0	0	—
2	23rd August, 1947 ..	83	—	0	5	0
3	30th September, 1947	16	0	0	10	0
4	28th May, 1948 ..	56	0	0	0	—
5	1st June, 1948 ..	82	0	0	0	—
6	4th June, 1948 ..	97	0	0	0	—
7	30th July, 1948 ..	70	0	0	0	0
	Mean	62·7	0	0	0·50	0

On the grounds of host-plant preference alone one may therefore conclude that the *Thomasiniana* sp. from blackberry is quite distinct from *T. theobaldi*. It also seems reasonable to recognise two strains within the present species *T. oculiperda*, one favouring apple and the other rose. *T. crataegi* appears to have nothing in common with the other members of the group.

TABLE IV.

Trials on host-plant preference, *T. oculiperda*, from rose.

Trial No.	Date commenced	Apple	Blackberry	Raspberry	Rose
		Eggs			
1	16th May, 1948	225	2	0	61
2	18th May, 1948	7	0	0	23
3	21st May, 1948	93	—	—	63
	Mean	53·6	0·56	0	44·2
		Larvae			
1	16th May, 1948	0	0	0	30
2	18th May, 1948	4	0	0	31
3	21st May, 1948	13	—	—	37
4	26th May, 1948 ..	27	—	—	35
5	26th May, 1949 ..	157	—	—	156
	Mean	9·6	0	0	45·3

TABLE V.

Trials on host-plant preference, *T. crataegi*.

Trial No.	Date commenced	Apple	Blackberry	Raspberry	Rose	Hawthorn
		Eggs				
1	8th September, 1947	0	—	0	0	51
2	18th May, 1948 ..	0	0	0	0	91
	Mean	0	0	0	0	68·7
		Larvae				
1	8th September, 1947	0	—	0	0	32
2	18th May, 1948 ..	0	0	0	0	137
	Mean	0	0	0	0	67·2

Timing of Spring Emergence.

All members of the group have a multivoltine life-cycle, spending the winter as resting larvae in cocoons in the surface soil. Pupation takes place in early spring and midges may begin to emerge at any time from late April to early June, largely depending on the weather and on topography. In the insectary, where the influence of the latter can be ignored, there have been consistent differences in the relative times of first and peak emergence of midges from the various host-plants. Figures for *T. crataegi* are not available, but over a period of four years the order of emergence of midges from the other host-plants has been substantially the same, the normal sequence being raspberry, rose, blackberry, apple. *T. theobaldi* again showed a contrast with the midge from blackberry by emerging at least seven days ahead of it; the rose strain of *T. oculiperda* preceded the apple strain by a similar margin.

TABLE VI.

Dimensions of *Thomasiniana* spp. in millimetres.

	T. oculiperda (apple strain)	*Thomasiniana* sp. from blackberry	*T. oculiperda* (rose strain)	*T. theobaldi*	*T. crataegi*
			Length of imagines (male)		
Range	1·0 – 1·49	0·96 – 1·49	0·91 – 1·87	1·25 – 1·78	1·37 – 1·99
Mean	1·24	1·24	1·37	1·41	1·72
			Length of imagines (female)		
Range	1·16 – 2·04	1·12 – 1·80	1·0 – 2·37	1·38 – 2·16	1·54 – 2·74
Mean	1·54	1·52	1·80	1·78	2·10
			Length of larvae (instar III)		
Range	1·99 – 3·00	1·77 – 3·06	1·78 – 3·35	1·62 – 3·28	1·70 – 4·27
Mean	2·48	2·37	2·75	2·48	2·98
			Breadth of larvae (instar III)		
Range	0·48 – 0·71	0·36 – 0·73	0·43 – 0·83	0·48 – 0·94	0·49 – 1·20
Mean	0·56	0·56	0·63	0·73	0·73

Morphological Data.

Clear-cut differences within this group are very few and the only obvious distinctions are best seen in living material. *T. crataegi*, for example, appears larger, darker and more sluggish than the other species and its larvae are also larger and of a paler shade of pink. It has also been noticed that about 7 per cent. of the larvae of *T. theobaldi* are of an orange colour, while the rest are of the normal pink; it has been shown experimentally (Pitcher, 1952) that these larvae do, in fact, belong to the same species. *T. theobaldi* is the only member of this group known to produce larvae of two colours in this way.

In the hope of revealing some less obvious differences, a number of comparative measurements have been made of parts of imagines and larvae. Measurement of overall size is of little value in determining the species of an individual because of the considerable variations occurring within a species due to nutrition and, in the case of larvae, to age. Table VI, however, shows that differences may be found between groups of individuals.

Analysis of the figures for imagines confirmed the larger size of *T. crataegi* and showed a contrast between the two strains of *T. oculiperda* and between *T. theobaldi* and the midge from blackberry (bracketed figures do not differ significantly). The figures for larvae were not analysed, but the larger size of *crataegi* is again apparent and there is also a suggestion that *theobaldi* is the broadest in proportion to its length.

Examination of antennae, male genitalia and wing/leg length ratios of imagines have shown little contrast, except in the case of the elongation on the terminal antennal segment, which, especially in the male, is usually more prominent in the midge from blackberry than in the others. Measurements of the rigid chitinised parts of third-instar larvae have been more satisfactory, especially when the relative lengths of certain abdominal setae are considered. The more useful of these measurements are summarised in Table VII; those showing no significant difference are bracketed together.

There is little contrast in the head-capsule widths within the group; these figures have not been analysed but it is noteworthy that *T. crataegi*, the larva with the largest body, appears to have the smallest head capsule. This species also stands out prominently when the lengths of the lateral abdominal setae are considered. On either margin of the abdomen all species in the group bear a pair of setae on segments 1 to 8 and a single seta on segment 9. In *T. crataegi* the setae on segments 1 to 8 are shorter than in the other species but those

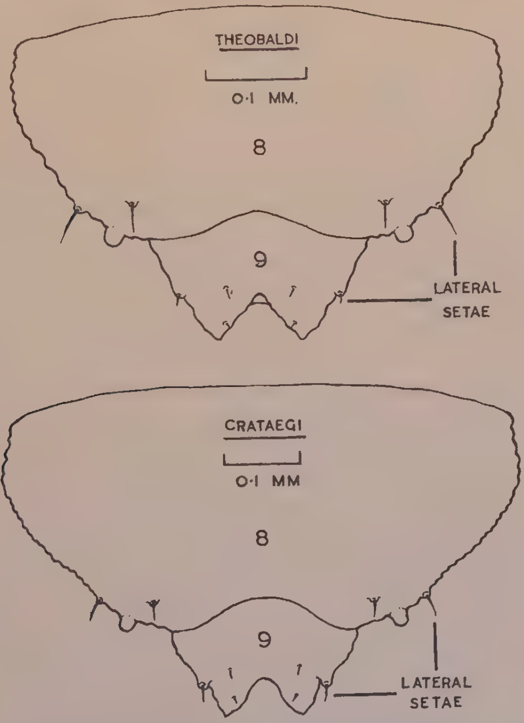


Fig. 1.—Comparison of the length of lateral setae on the terminal segments of mature larvae of *Thomasiniana theobaldi* and *T. crataegi*.

on segment 9 are longer. This difference can be readily seen with a $\frac{2}{3}$″ objective (fig. 1), and can be demonstrated numerically by measuring the more dorsal of the pair of setae on segment 1 (A1D) and the single seta on segment 9 (A9) and expressing them as the ratio A1D/A9. It will be seen from Table VII that in every case the figures for *T. crataegi* differ significantly from those for other species. There is also a significant difference in the length of the A9 seta between the two strains of *T. oculiperda*, but apart from this the members of the group are remarkably uniform.

TABLE VII.

Dimensions of parts of third-instar larvae of *Thomasiniana* spp. in microns.

	T. crataegi	*T. oculiperda* (apple strain)	*T. oculiperda* (rose strain)	*T. theobaldi*	*Thomasiniana* sp. from blackberry
	Head-capsule width				
Range	50·0—60·3	53·4—60·3	55·1—63·2	55·1—62·1	55·1—62·1
Mean	56·2	56·9	58·3	59·7	57·7
	Length of lateral abdominal setae Segment 1, dorsal (A1D)				
Range	13·8—27·6	17·3—31·0	13·8—31·0	20·7—31·0	20·7—27·6
Mean	18·9	24·1	25·2	24·8	24·1
	Segment 9 (A9)				
Range	15·5—24·1	10·4—20·7	6·9—12·1	6·9—12·1	6·9—13·8
Mean	19·3	15·5	9·31	8·61	8·61
	Ratio— A1D/A9				
Range	0·8—1·6	0·8—2·7	2·0—4·0	2·0—3·8	2·0—4·0
Mean	1·01	1·65	2·82	2·92	2·95

Specific Status of the *Thomasiniana* sp. from Blackberry.

Biological differences between the midge from blackberry and *T. theobaldi* have been shown by the trials on host-plant preference and by a comparison of the emergence times of the spring generations. The demonstrable morphological differences were less striking, but the presence of larvae of two colours in *T. theobaldi* only and the longer terminal elongation of the antennae of the midges from blackberry suggested that the two were not identical.

A series of cross-breeding experiments was carried out to see if these were strain differences within a species or whether there were two distinct species involved. Twenty attempted cross-matings, ten in each direction, yielded no eggs, whereas in self-matings under comparable conditions it is usual for at least 50 per cent. of the pairs to produce eggs. It has therefore been concluded that the midge from blackberry can be put forward as a new species of the genus *Thomasiniana*. Accordingly the species is named *fruticosi* and the common name " Blackberry Cane Midge " is proposed. The following is a formal description of the new species.

Thomasiniana fruticosi, sp.n.

Male. Length about 1·25 mm. Antennae: 2 + 12, first and second flagellar segments fused, each flagellar segment with a basal subglobular node bearing one ring of circumfila with regular loops reaching nearly to the base of the distal node and an irregular whorl of long setae, and a distal elongated node bearing two rings of circumfila, in the basal ring the regular loops extend about as far as the insertion of the distal ring, the regular loops of which are longer, usually reaching the basal node of the next segment; between the two rings of circumfila lies an irregular whorl of long setae; the basal and distal nodes of each segment are separated by a stem, which often bears a slight medial swelling, and each distal node bears a distinct neck; the stem of the third flagellar segment is 1 to 1½ times as long as broad and the neck 2 to 2½ times as long as broad, the neck longer than the stem; the stem of the tenth flagellar segment is 2 to 3 times as long as broad and the neck about 4 times as long as broad; the distal node of the twelfth flagellar segment bears a setose elongation which is usually longer than broad. Palpi: basal segment quadrate, the second, third and fourth segments are, respectively, about 2½ to 3, 2½ to 4 and 3 to 5 times as long as wide. Wings: hyaline, with many dark hairs, third vein reaching margin at the tip, fifth vein forked, almost at a right angle. Legs: pale with dark hairs, claws bent at right angles, with basal tooth, empodium small. Genitalia: basal clasp segment stout, 2 to 2½ times as long as broad, distal clasp segment tapering, dorsal lamella with deep V-shaped emargination, each lobe broadly rounded; ventral lamella with U-shaped emargination, lobes rounded but less so than in dorsal lamella.

Holotype: Cecid. 4425.†

Paratypes: Cecid. 4424, 4426, 8938–9,* 8940–2.

Other specimens: Cecid. 8937, 8943–5; and five additional slides.*

Female. Length about 1·5 mm. Antennae 2 + 12, first and second flagellar segments fused, each flagellar segment cylindrical with short transverse neck, with two whorls of setae, those in the basal whorl being much the longer and two rings of applied circumfila united by a longitudinal thread, the third flagellar segment is about twice as long as wide and the twelfth flagellar segment 2½ to 3 times as long as wide, including the setose distal prolongation. Palpi: as in male, but slightly more slender. Ovipositor: long, very extensile, the paired lamellae elongate ovoid, with long fine setae, the basal lamella very small. Otherwise about as in male.

Allotype: Cecid. 8950.

Paratypes: Cecid. 4427–30, 8947–9, 8955–6.*

Other specimens: Cecid. 8946, 8951–4, 8957–8; and five additional slides.*

Larva. Pink, typical *Thomasiniana* roundedly bifid sternal spatula and anal segment.

Cecid. 4377–9.

Habitat: Canes of wild blackberry, *Rubus fruticosus.*

Type locality: Wisley, Surrey, England.

---

† The numbers refer to slides indexed in the Barnes collection at Rothamsted.
* Slides marked with an asterisk are lodged at East Malling.

Status and Economic Importance of all Species.

Both on biological and morphological grounds it is clear that *T. crataegi* is distinct from all the other members of the group. The remainder, although easily separable on biological grounds, are obviously very close morphologically. They are, however, not without certain biological affinities. All, for example, contain some individuals which can live on rose, although the rose strain of *T. oculiperda* is the only member with a preference for this host. On grounds of preference for other host-plants, they fall easily into two pairs, the *Rubus*-favouring *T. theobaldi* and *T. fruticosi* on the one hand and the rose and apple strains of *T. oculiperda* on the other. *T. theobaldi* and *T. fruticosi* have now been shown to be distinct species. It has also been possible to show differences in morphology and spring-emergence time between the two strains of *T. oculiperda* which are at least as pronounced as those between *T. theobaldi* and *T. fruticosi* and in time it may be found that these are specific and not strain differences. It is clear that much more work, entailing many cross-matings and attempts to select out specialised host races from field populations, needs to be done before the detailed interrelationship of the members of this group can be fully revealed. However, on the evidence at present available, it does not seem unreasonable to suggest that this is a group of strains and species still in the course of evolution. Quite possibly, as all have rose as a common host-plant, they all stem from the rose strain of *T. oculiperda*. In this connection it is interesting to note that this is the strain showing the greatest adaptability, being the only one which is known *readily* to accept a host-plant of a genus (*Pyrus*) other than that of its preferred host (*Rosa*). The apple strain of *T. oculiperda* seems to be only slightly removed from the rose strain, but *T. theobaldi* and *T. fruticosi* are more distant and may well have sprung from a common offshoot of *T. oculiperda* which became adapted to *Rubus* spp.

It is now possible to make a more critical assessment of the potentialities of each midge as a horticultural pest. *T. crataegi*, although widely distributed, is confined to hawthorn, which it does not injure sufficiently to affect its usefulness as a hedging plant.

T. oculiperda contains at least two biological strains, on apple and rose, respectively, both of which can live on either host and can thus cause injury to the budded nursery stock of either. It is likely, however, that the apple strain is predominant in apple-growing areas, where it lives mainly as a casual inhabitant of broken branches of established apple trees. Midges flying from this situation may damage apple, rose and, possibly, fruit-tree rootstocks other than apple if budding is carried out during the emergence of a summer generation. Hedgerow roses probably hold the main reservoir of the rose strain, although established rose nurseries may support a small residual population which lives in small cuts and abrasions of the bark when no budding slits are available. Both *T. theobaldi* and *T. fruticosi* could also cause some damage to rose, but this is unlikely to be extensive.

In the case of *T. theobaldi*, raspberry is the only host of economic importance, and serious damage will occur only on varieties whose bark readily splits and peels. Loganberry and Himalaya Giant blackberry may harbour a few larvae, chiefly in broken canes, but no important damage is likely. *T. fruticosi* lives almost exclusively on hedgerow blackberries. Cultivated blackberries may occasionally be attacked but no economic damage is likely as the bark of blackberry does not split extensively, so that larval colonies will be largely confined to broken canes. Raspberries may be lightly attacked if grown in the presence of many wild blackberries.

Parasites.

In the course of these and other investigations the following parasites have been recorded:—

T. crataegi: *Leptacis* sp., *Inostemma* sp.
T. oculiperda (apple strain): *Leptacis* sp., *Trimorus* sp., *Inostemma* sp.
T. oculiperda (rose strain): genus near *Lamprotatus*, *Inostemma* sp.
T. theobaldi: *Leptacis* sp., *Piestopleura catillus* (Wlk.), *Tetrastichus inunctus* (Nees) (for biology see Pitcher, 1952).
T. fruticosi: *Aphanogmus* ? *fumipennis* Thoms.

Summary.

A comparison is made of all the members of the genus *Thomasiniana* Strand at present known from Rosaceous host-plants, namely *T. oculiperda* (Rübs.), the Red Bud Borer; *T. theobaldi* Barnes, the Raspberry Cane Midge; *T. crataegi* Barnes, the Hawthorn Stem Midge and a hitherto undescribed species from wild blackberry. Although morphologically very similar, each can be readily distinguished in trials on host-plant preference. By this means it has also been shown that there are two strains, favouring apple and rose respectively, within the present species *T. oculiperda*. Other biological and some morphological evidence is given, supporting the above conclusions, and on this basis the midge from blackberry is put forward as a new species for which the names *Thomasiniana fruticosi*, sp. n. and "Blackberry Cane Midge" are proposed and a formal description given. The biological and economic status of each species or strain is discussed and a list of the known parasites given.

Acknowledgements.

The writer wishes to thank Dr. H. F. Barnes of Rothamsted Experimental Station for his valued help and advice; Mr. G. E. J. Nixon of the Commonwealth Institute of Entomology for identifying the parasites, and Mr. G. H. Freeman for carrying out statistical analyses.

References.

Barnes, H. F. (1931). Observations on gall midges affecting fruit trees.—J. S.-E. agric. Coll. Wye, **28,** pp. 170–177.

Barnes, H. F. (1939). Some gall midge species and their host plant range.—Ann. appl. Biol., **26,** pp. 318–347.

Barnes, H. F. (1944). Investigations on the Raspberry Cane Midge, 1943–44.—J. R. hort. Soc., **69,** pp. 370–375.

Barnes, H. F. (1953*a*). The biological approach to the species problem in gall midges (Dipt. Cecidomyidae).—Ann. ent. fenn., **19,** pp. 2–24.

Barnes, H. F. (1953*b*). Description of the new gall midge found by M. R. Pussard on lavender, together with notes on the damage caused by some other species (Dipt. Cecidomyidae).—Bull. Soc. ent. Fr., **58,** pp. 125–128.

Grandi, G. (1951). Introduzione allo studio dell' entomologia, **2,** p. 310. Bologna, Edizioni Agricole.

Pitcher, R. S. (1952). Observations on the Raspberry Cane Midge (*Thomasiniana theobaldi* Barnes). I. Biology.—J. hort. Sci., **27,** pp. 71–94.

Pitcher, R. S. & Webb, P. C. R. (1952). Observations on the Raspberry Cane Midge (*Thomasiniana theobaldi* Barnes). II. "Midge blight", a fungal invasion of the raspberry cane following injury by *T. theobaldi*.—J. hort. Sci., **27,** pp. 95–100.

Rao, S. N. (1951). Descriptions of two new genera and nine new and one known species of gall midges (Itonididae: Diptera) from India.—Indian J. Ent., **11**, pp. 109–127.

Wilson, G. Fox & Green, D. E. (1944). Observations on two raspberry troubles. —J. R. hort. Soc., **69**, pp. 79–86.

THE PERSISTENCE AND FATE OF DDT ON FOLIAGE.

I.—THE INFLUENCE OF PLANT WAX ON THE TOXICITY AND PERSISTENCE OF DEPOSITS OF DDT CRYSTALS.

By P. E. Burt and J. Ward

Department of Insecticides and Fungicides, Rothamsted Experimental Station, Harpenden, Herts.

Introduction.

The possible causes of loss of toxicity of insecticidal deposits on foliage may be summarised under three headings: mechanical losses, losses due to other physical processes and losses due to chemical change of the insecticide.

Mechanical losses include removal by wind or by brushing of leaves against one another or by washing of the foliage by rain; loss due to death of the foliage and replacement by new growth, or to growth of the leaf and consequent attenuation of the deposit; and masking of the deposit by a layer of dust or other foreign material such as exudate from Aphids or scale insects.

Losses due to other physical processes include changes in toxicity due to alteration of the physical nature of the film, *e.g.*, a change in the degree of adhesion of insecticide particles, crystallisation of a solution, or liquefaction of a solid; penetration of the insecticide into the leaf, either by diffusion or by material entering the stomata; and volatilisation of the insecticide.

Losses due to chemical change of the insecticide include decomposition caused by ultra-violet light; decomposition induced by catalysts or occurring spontaneously; and decomposition caused by exposure to air or moisture.

The object of the work to be described in a series of papers, of which this is the first, was to determine the importance of some of these factors in causing loss of insecticidal power of DDT films, particularly under tropical conditions.

Reports of the duration of the persistent effect of DDT on plants and other surfaces vary widely. Lindgren & Boyce (1944) found that DDT dissolved in kerosene or other petroleum spray oils and applied as an oil-water emulsion to *Citrus* trees, continued to be effective against the nymphs of California Red Scale, *Aonidiella aurantii* (Mask.), for 60 days. Brunson & Koblitsky (1953) found in two experiments that DDT applied to peach foliage as a wettable powder was lost to the extent of 85 per cent. and 53 per cent. in three weeks. Symes & others (1948) found that, when DDT was applied to two different species of plant as an emulsion consisting of DDT dissolved in heavy solvent naphtha and emulsified in water, after eight weeks little reduction in the toxicity of the deposit to tsetse flies had occurred. A deposit from a solution of DDT in diesel oil, however, was reduced to approximately 20 per cent. of the original density in three weeks. Hadaway & Barlow (1949) reported almost complete loss of effect in one week with deposits derived from a solution of DDT in 50:50 kerosene: cottonseed oil on avocado-pear foliage in the open.

The extent of mechanical loss of persistent insecticides due to wind and rain was studied by Mistric & Gaines (1953). They found that wind, rain and also high temperature each increased the rate of loss, and showed that, with the materials used (heptachlor, toxaphene, dieldrin, aldrin, endrin and BHC), losses caused by high temperatures were increased when the rate of ventilation was increased. Decker & others (1950) studied the rate of loss of activity of a number of insecticides (aldrin, dieldrin, chlordane, toxaphene, lindane, DDT and parathion) on crops. They believed that, in the absence of rain, the rate of loss was correlated with the vapour pressure of the insecticide. Of the insecticides tested, toxaphene and chlordane were the most resistant to losses caused by rain.

A deposit of insecticide on a leaf becomes attenuated as the leaf grows. A vigorously growing plant may also produce new leaves after an application of insecticide and so grow out of the protection of the insecticidal film. Sloan & others (1951) found that, fourteen days after lettuces had been treated with DDT oil-emulsion or wettable-powder sprays, 94 per cent. of the DDT per unit area of the leaves had been lost. They attributed 73 per cent. loss to the growth of the plants, the remainder being due to the effects of weathering. Hopkins & others (1952) found almost complete loss of all the insecticides which they tested (parathion, aldrin, lindane, benzene hexachloride and DDT, all applied as dusts), in thirty days when applied to a crop of alfalfa. The growth of the crop was rapid and must have contributed to the loss. Growth of the crop thus sets a limit to the period of effectiveness of a single application of insecticide, and in the case of a crop which is actively growing and rapidly producing new shoots, this period may be only a week or two.

Only slight penetration of DDT into leaves was reported by Symes & others (1948) when the insecticide was applied dissolved in heavy solvent naphtha and emulsified in water. If the DDT was applied as a 5 per cent. solution in diesel oil, however, about 30 per cent. of the DDT could not be removed by washing with benzene, but was recovered by extracting the leaves exhaustively with solvent. Hadaway & Barlow (1949) also reported penetration of DDT into leaves when the insecticide was applied to the foliage as a 5 per cent. solution in 50:50 kerosene:cottonseed oil. Stafford & Hinkley (1946) observed that olive oil obtained from olives which had been sprayed with a mixture of a DDT wettable powder and a light soluble oil contained DDT. Gunther, Lindgren, Elliot & La Due (1946) sprayed *Citrus* foliage with DDT dissolved in kerosene both with and without various auxiliary solvents, and showed that the DDT penetrated into the foliage to a considerable extent, but that some DDT returned to the surface of the leaves a few days after spraying. Griffiths & Stearns (1949) found that when *Citrus* groves were sprayed with DDT three or four times in the summer, by November most of the DDT retained by the foliage had been absorbed into the leaf tissue. Their method of distinguishing between superficial and absorbed DDT may not have been entirely satisfactory. Kozlova & Dvortsova (1952) showed that DDT applied to the soil could be absorbed by the roots of plants and detected in the leaves by its toxic effects, while Huffaker (1948) found that when a dispersion in water of DDT dissolved in polyethylene glycol was passed into a bean plant by means of a cotton wick threaded through the stem, toxic amounts of DDT appeared in the leaves. He also showed that DDT was absorbed into bean plants when pellets of DDT mixed with polyethylene glycol or of DDT mixed with lanolin were applied to the leaves. Plummer & Carter (1946), however, found that after six sprayings of a potato crop with 0·1 per cent. DDT as a wettable powder, no DDT was detectable in the tubers. Working with plants shaded from direct sunlight in a glasshouse, M. J. Way (private communication) showed that there was a loss of contact activity from cabbage plants which had been sprayed with a crystalline suspension of DDT. The loss was not fully accounted for by the growth of the cabbage plants. When the leaves were tested for activity as a stomach poison, however, there did not appear to have been any loss; the loss of contact activity may have been due either to a change in the physical state of the poison, or to its absorption into the leaf.

There are two ways by which an insecticide can penetrate into the tissue of a leaf. Either the medium in which the insecticide is applied can enter the leaf carrying the poison with it, or, after the medium has dried, the insecticide deposited on the outside of the leaf can diffuse through the cuticle or through the stomata into the leaf tissue. Fogg (1948*a*, *b*) has shown that aqueous media do not pass through the stomata, even when they contain wetting agents, while oils readily pass through into the intercellular spaces of the leaf. This agrees with the findings of Symes & others (1948) mentioned above, who found that penetration of DDT into leaves was greater when it was applied as an oil solution than as an emulsion or wettable powder. The evidence for penetration of DDT through the cuticle apart from solvent is contradictory; without further work it is not possible to decide whether or not it occurs.

Losses caused by chemical decomposition of DDT have been attributed to the action of catalysts, to reaction with basic substances such as lime, or to the effect of ultra-violet light. The effects of catalysts and of light have not always been successfully distinguished, as the heating caused by sunlight also accelerates catalytic decomposition. Decomposition of DDT residues derived from kerosene emulsions and wettable concentrates on *Citrus* fruit was studied by Gunther, Carman & Elliot (1948). They found crystalline deposits of almost non-toxic material after periods up to 60 days, and believed that decomposition had been induced by sunlight and by the presence of catalytic impurities such as iron salts. They considered that the first step in the decomposition was the removal of HCl from the DDT molecule, giving dichlorodiphenyldichloroethylene, and they showed that this reaction was inhibited by picolinic acid. Burgess & Sweetman (1949) showed that the toxicity of deposits on wire gauze of DDT derived from a kerosene solution decreased more rapidly at 37°C. than at 23°C., and more rapidly in moist air than in dry. The loss they found at 37°C. may have been partly due to volatilisation. Teotia & Dahm (1950) studied the loss of effectiveness of deposits of aldrin, chlordane, dieldrin, lindane and parathion on wood, paint and glass surfaces, and found that high temperatures and weathering accelerated the loss. Gahan & others (1945) found that, at a density of 50 mg. per sq. ft., deposits of DDT on wood, whether applied as kerosene solutions, as emulsions or as suspensions, remained effective after twenty-four weeks' exposure to sunshine. Working with exposures to sunlight of up to 64 hours, Chisholm & others (1949) found that deposits from DDT wettable-powder suspensions remained toxic in the absence of alkaline, or iron-containing "inert" diluents, but suffered severe loss in the presence of these substances. Deposits from insecticidal emulsions in which the DDT was dissolved in an organic solvent rapidly lost their effect in sunlight. Wichman & others (1946) found that crystalline DDT was resistant to irradiation by a powerful ultra-violet lamp, but that solutions of DDT in benzene were rapidly decomposed. Decomposition, once started, continued even after the benzene had evaporated. Fleck (1948) confirmed these findings, and showed that the rate of decomposition of DDT in solution under the influence of ultra-violet light depended on the type of solvent. He also showed (Fleck, 1949) that decomposition by ultra-violet light gave a different product depending on whether air was present or absent, and that dehydrochlorination was not necessarily the first step involved. It seems possible that the processes which occur under the influence of short-wave ultra-violet light in the laboratory are not necessarily the same as those induced by sunlight, though Lindquist & others (1946) found that deposits from DDT suspensions persisted longer when exposed to sunlight than did deposits of DDT in the presence of high-boiling solvents.

Much of the more detailed work reviewed above on the decay of insecticidal deposits has been concerned with surfaces other than foliage. The causes of losses which occur independently of the nature of the surface are therefore rather better understood than those which are due to some property of the foliage itself. It was decided to begin this work by finding whether the superficial waxy layer on foliage had any effect on the toxicity or persistence of deposits of DDT overlying it, and in particular whether the DDT could dissolve in the wax and diffuse through it into the leaf tissue. The first two papers of this series are concerned with this problem and with the volatility of DDT deposits on glass or leaf surfaces, the importance of which became obvious in the course of the work.

Methods.

The leaves and fleshy stems of most plants are covered with a layer of wax. Insecticides sprayed on to plants therefore rest on the wax layer. A crystalline, oil-soluble insecticide, such as DDT, might slowly dissolve in the wax, thus penetrating at least the outermost layer of the plant. Such a physical change might affect the contact toxicity of the insecticide by making it less readily picked up by an insect in contact with the plant. Further penetration into the tissue of the plant might also occur, resulting in complete loss of contact toxicity. To simplify the problem and to reduce the experimental difficulties, it was decided first to study the changes occurring in DDT deposits on glass plates coated with plant wax, using similar deposits on plain glass for comparison.

The wax films on plants of different species vary considerably in thickness, in the chemical and physical properties of the wax, and in the texture of the surface. Choice of waxes for this work was limited, as they had to be available in fairly large quantities; it was also desirable that at least one of the waxes should be derived from a plant which could itself be used in subsequent experiments for the study of loss of toxicity of deposits on living leaves. Cabbage wax (M.P. 62–64°C.) was chosen, as it occurs in a relatively thick layer and was easy to obtain in quantity, and because cabbage was a suitable plant for the later work. Carnauba wax was tried, but it proved difficult to obtain a smooth surface on the wax film. Sisal wax (M.P. 85–92°C.) was found to be suitable, and was made the second choice.

The thickness of the wax layer on cabbage was estimated by extracting the wax from a measured area of leaf and weighing it. The estimates of thickness so obtained ranged from about 0·2 μ on young leaves to 0·45 μ on old ones. It was decided to deposit films about 0·5 μ thick on the glass plates, so as to have the thickest possible layer without departing too greatly from that found on cabbage leaves. The layer of wax on the other plants examined was found to be very much thinner.

The temperature to which deposits of DDT on foliage may be exposed is the temperature of the surface of the leaves, and in hot sunshine this may be considerably greater than the air temperature. Measurements recorded in the literature (Curtis, 1936, 1938; Wallace & Clum, 1938; Munger, 1948; Waggoner & Shaw, 1952) show that a difference of 10°C. or more between air and leaf temperatures is possible. We carried out a few measurements on a cabbage plant, and found a maximum difference of 7°C. when the experiments were conducted out of doors, and of 10°C. in a greenhouse where the plant was protected from the wind. These measurements were made by thrusting a fine thermocouple into the flesh of the leaf (or by attaching a thermocouple to the back of the leaf by means of adhesive tape, which gave the same reading), and presumably were rather lower than the temperature of the insolated surface. It seemed reasonable to suppose, therefore, that under some tropical conditions foliage might be heated by the sun to 40–45°C. It was decided to choose a temperature of 43°C. as the temperature at which to investigate the behaviour of DDT deposits. For comparison, work was also done at 18°C.

Preparation of plates coated with sisal wax.

Sisal wax was produced by extracting sisal leaf-cuticle (obtained through the courtesy of the A.S.P. Chemical Co. Ltd., of Gerrards Cross, which processes sisal commercially) with benzene in a large soxhlet extractor. The solvent was removed by evaporation, and the wax was powdered. Glass plates of area 8·0 by 8·0 cm. were coated by spraying them in the Potter tower (Potter, 1952) with a 0·3 per cent. solution of sisal wax in toluene, heated to 60°C. to reduce crystallisation of the wax round the jet orifice. Two coats, each using 10 cc. of solution, were applied, allowing the plates to dry between coats. By weighing plates before and after spraying, it was shown that the wax layer was of the required thickness.

Preparation of plates coated with cabbage wax.

Originally, a method similar to that used for sisal wax was used, but later it was found more convenient to spray the plates by means of a paint-spray operated by compressed air, using the method developed for spraying insecticide on to living leaves. This will be described in a later paper. Depending on the ambient temperature, each wax film was built up of two or four separate applications, each application being insufficiently heavy to cause coalescing of the drops of spray on the plate and consequent running of the wax solution. Each coat was dried before the next was applied. After spraying, the plates were heated for a few minutes in an oven at 70°C. until the wax layer just melted. When examined microscopically, the wax layer could be seen to be continuous over the glass, though its surface was somewhat irregular.

The cabbage wax was prepared by collecting the large old leaves left in the field when cabbage was cut for market, washing with water to free them of mud and dust, then dipping them one at a time into two successive baths of toluene maintained at 60°C. The wax solution was concentrated by distillation under reduced pressure on a water-bath. The concentrated solution was centrifuged while still hot and the remainder of the solvent removed from the resulting clear liquid by prolonged heating in a dish on a steam-bath. Two sacks of leaves yielded about 20 gm. of cabbage wax (M.P. 62–64°C.). Wax obtained by scraping a cabbage leaf had the same melting point. Melting points were taken with a Kofler micro heating stage.

Application of the insecticidal deposit.

The DDT formulation used was as simple as possible, a suspension of DDT crystals in a medium composed of 90 per cent. water, 10 per cent. ethanol, containing 0·1 per cent. sulphonated lorol. The crystals were prepared according to the method of McIntosh (1947) and were predominantly of one size, needles 50 μ long and about 1 μ in diameter. Recrystallised DDT (M.P. 107–109°C.) was used in the preparation.

Deposits of different densities were made by diluting the suspensions made in this way with 0·1 per cent. sulphonated lorol in 90 per cent. water, 10 per cent. ethanol so that the deposits differed from one another only in the amount of DDT present. In the early part of the work, the suspension was sprayed on to the plates by means of the Potter tower. Later, the method of spraying used for living leaves (and referred to above in connection with the production of wax-coated plates) was used, as large numbers of plates could be produced more rapidly in this way. In either case, it was important to apply the spray in several coats, allowing the plates to dry between coats, as an uneven deposit resulted if the plates became too wet during spraying.

Method of biological testing.

The insecticidal activity of the deposits was tested by confining small numbers of adult *Tribolium castaneum* (Hbst.) on the surfaces inside small glass collars. The insects remained on the surfaces for 24 hours, were then removed, kept three days, examined on a warm plate, and the dead counted. The test insects were reared at a temperature of 27°C. All tests with results intended for direct comparison were carried out at the same time, with insects of identical age, and where the total number of insects required necessitated the use of more than one culture, the insects from all the cultures used were carefully mixed before use. Hence in any one test all the insects used were of the same age, but no particular insect age was adhered to throughout the tests.

Where possible, the probit transformation of Bliss (1934), with the calculation procedure suggested by Finney (1947), was applied to the mortalities so obtained. Where duplicate deposits had been prepared and analysed, the independent variable was the logarithm of the density of the DDT deposit as found by analysis. Where there were no such analytical figures, the logarithm of the concentrations of the solutions sprayed was used as the independent variable.

This biological test was used in experiments (described below) in which plates, either plain glass or wax-coated, were sprayed with deposits of DDT and then subjected to a period of treatment the conditions of which varied from one experiment to another. The toxicity of the deposits was then assessed by confining insects on them in the manner already described. A probit line was then constructed from the results of each test, using as the independent variable either the density of the deposit before storage, or the concentration originally sprayed. There is no theoretical justification for the use of the probit transformation in these cases, as the losses from deposits due to volatilisation during storage at high temperatures are not proportional to the original deposit densities (see Table VIII). The transformations, however, gave homogeneous lines in practice, and permitted the calculation of the *original* deposit density that, when tested in the given treatment conditions, would give a 50 per cent. kill.

When this procedure is used, a decline in the toxicity of the deposit shows itself as an increase in the calculated value of the original dose that, when tested after undergoing the given treatment, produces a 50 per cent. kill. This value is referred to as the LD50 for the particular treatment. In Tables I and II, the results are given as log relative potencies, taking the potency (*i.e.*, the reciprocal of the LD50) of freshly sprayed glass plates as standard. The log relative potency is obtained by subtracting the log LD50 calculated for the treatment from that found for freshly sprayed glass plates. The standard error of a log relative potency was computed by adding the variances of the two log LD50's from which the relative potency was derived and taking the square root of the sum.

Method of chemical estimation.

Wax-coated plates bearing DDT deposits were extracted by heating with benzene in a crystallising dish on a steam-bath until the benzene just boiled. The plate and dish were then rinsed with two further washes of benzene. Plates carrying only the DDT deposit were washed with cold acetone, and 5 mg. of stearic acid was added to prevent volatilisation of DDT when removing the solvent. Thereafter the Schechter-Haller method, modified in a way similar to that proposed by Downing & Norton (1951), was used.

Persistence of DDT Deposits stored in the Dark at different Temperatures.

Persistence of DDT on sisal wax.

Glass plates were coated with films of sisal wax and sprayed with DDT suspensions of seven different concentrations. Plain glass plates were also sprayed with the same suspensions. This was done on three different occasions, so that biological tests could be carried out simultaneously on freshly sprayed plates and on plates which had been stored in the dark for two different periods at two different temperatures. The storage temperatures were 43°C. and 18°C. The results are shown in Table I. A further experiment, in which the plates were stored for 26 days before testing, is also reported in Table I, but as the biological testing was not carried out simultaneously with that of the earlier tests, the relative potencies may not be comparable with those of the shorter exposure periods.

TABLE I.

Changes in toxicity of DDT deposits on glass plates, both plain and coated with sisal wax, on storing at 18°C. and at 43°C.

Days' storage	Glass surface		Wax surface	
	Stored at 18°C.	Stored at 43°C.	Stored at 18°C.	Stored at 43°C.
0	0·00		+0·55±0·08	
2	+0·14±0·08	−0·18±0·06	+0·62±0·13	−0·16±0·11
8	+0·36±0·07	−0·62±0·08	+0·63±0·06	−0·66±0·10
26	−0·09±0·07	negligible kill	0·00±0·08	negligible kill

Results are log relative potencies, the potency of fresh deposits on glass being taken as standard. The plates stored 26 days were tested at a different time from the others, and with a different batch of insects.

DDT deposits on sisal wax appear to be inherently about four times as toxic as those on glass. On storing at 18°C., the deposits on wax maintained their toxicity more or less unchanged, while those on glass increased in toxicity, at least up to eight days from the date of spraying. This increase in toxicity after storage has been encountered in subsequent experiments, but has not yet been explained. The plates kept at 43°C. lost toxicity rapidly. After eight days the deposits on glass and on wax surfaces were respectively one-quarter and one-sixteenth as toxic as the corresponding freshly sprayed plates. After 26 days, the toxicities were too small to measure.

Persistence of DDT on cabbage wax.

The experiment of storing plates, coated with sisal wax, at 43°C. was later repeated using plates coated with cabbage wax. In this experiment, the second

TABLE II.

Change in toxicity of DDT deposits on glass plates, both plain and coated with cabbage wax, on storing at 18°C. and at 43°C.

Days' storage	Glass surface		Wax surface	
	Stored at 18°C.	Stored at 43°C.	Stored at 18°C.	Stored at 43°C.
0	0·00		−0·12±0·04	
5	+0·31±0·11	−0·24±0·06	−0·05±0·07	+0·11±0·08
14	very high toxicity	approx. −0·7	+0·01±0·07	approx. −0·6

Results are log relative potencies, the potency of fresh deposits on glass being taken as standard, the median lethal density of such deposits being 0·675 microgm. per sq. cm.

method of application of the DDT deposits was used, so that up to nine plates could be sprayed with one DDT suspension at a time. Two of the plates were analysed immediately to give the rate of deposit of DDT; the remainder were used to study the rate of loss of toxicity by both chemical analysis and bioassay. The results of biological tests of the plates are shown in Table II, and the results of the chemical analyses in Table III. Results over 100 per cent. are due to differences in the deposit density on plates sprayed simultaneously.

The biological results again show an increase in toxicity of deposits on plain glass stored at 18°C. The batch of *T. castaneum* used in these tests was unfortunately unusually susceptible, due possibly to a short exposure to a high temperature during rearing; after 14 days at 18°C., the glass plates had become so toxic to the insects that even the lowest rate of deposit sprayed produced 95 per cent. kill and no LD50 was obtained. At 43°C., the glass plates again lost toxicity, and Table III shows that a simultaneous loss of DDT was occurring. The plates coated with cabbage wax, like those coated with sisal wax in the previous experiment, remained more or less unchanged in toxicity after storage at 18°C., but they were initially slightly less toxic than plain glass, whereas plates coated with sisal wax were initially more toxic. This difference could be due to the greater roughness of films made from sisal wax, which is apparent under the microscope. The plates coated with cabbage wax stored at 43°C. for 14 days had declined in toxicity as expected, but after only five days' storage the toxicity had apparently increased.

TABLE III.

Percentage of original deposit of DDT remaining on glass surfaces, both plain and coated with cabbage wax, after storage, as determined by analysis.

(a) Stored at 18°C.

Mean initial deposit (microgm./sq. cm.)	% of deposit remaining after:—			
	5 days		14 days	
	Glass	Wax	Glass	Wax
1·24	89	102	98	114
0·65	—	—	90	117
0·40	102	112	—	—

(b) Stored at 43°C.

Mean initial deposit (microgm./sq. cm.)	% of deposit remaining after :—			
	5 days		14 days	
	Glass	Wax	Glass	Wax
6·1	82	84	58	75
3·8	87	84	7	7
2·3	—	51	1	2

In these two experiments, both chemical and biological assay showed that at 43°C. a rapid loss of DDT from deposits on glass plates both with and without a wax coating had occurred. Since the presence of a film of wax on the glass did not significantly affect the rate or amount of loss, it seemed likely that the DDT had either volatilised or decomposed chemically.

Loss of weight of DDT deposits after storage at 43°C.

Glass coverslips, half of which had previously been sprayed with sisal wax, were sprayed with a suspension of DDT crystals, containing 0·1 per cent. DDT. The coverslips were kept at either 18°C. or 43°C. for 21 days, and all were weighed with a microbalance before and after being sprayed, and after storage. The results (see Table IV) were somewhat variable due to the very small weights of insecticide involved, but showed clearly that very considerable losses took place at 43°C. The losses from the waxed coverslips at 18°C. may have been due to removal of small amounts of wax from the film during manipulation. It was concluded that at 43°C. DDT was lost either by volatilisation or by decomposition into volatile degradation products.

TABLE IV.

Loss of DDT from deposits on coverslips, with and without a coating of sisal wax, kept at temperatures of 18°C. and 43°C. for 21 days. Original rate of application approx. 4·2 microgm./sq. cm. Results are corrected for change in weight of control coverslips.

Surface	Temperature (°C.)	% Change in wt. of deposit
Glass ..	18	+ 6 (mean of 5)
Glass ..	43	−74 (mean of 4)
Wax ..	18	−33 (mean of 4)
Wax ..	43	−87 (mean of 5)

Persistence of DDT Deposits kept in an Atmosphere saturated with DDT.

Plates, both plain glass and coated with cabbage wax, were sprayed with various concentrations of DDT crystal suspensions and kept in a desiccator at 43°C. over crystalline DDT, so that the atmosphere within was constantly saturated with DDT vapour. Plates, similarly treated, were kept unconfined in a constant temperature room at 18°C. Some plates were kept under these two sets of conditions for three days and others for 21 days. The spraying was done on different days, in such a way that the toxicities of the aged deposits could all be tested simultaneously. Other plates were sprayed with the DDT suspension on the day of testing to give the reference level of insect resistance. The results are summarised in Table V.

At 18°C. little or no loss of DDT occurred from either glass or wax surfaces. On glass kept in the desiccator at 43°C., a slight loss of DDT occurred but this was much less than had been found for plates kept at 43°C. in the free atmosphere. However, the waxed plates maintained at 43°C. in the desiccator suffered a considerable change. There was no decrease in toxicity at the higher concentrations, but an increase in toxicity at the lower concentrations was evident, particularly of the plates stored for 21 days. The waxed control plates, on which there was no initial deposit of DDT, were capable of killing 14 per cent. of the *T. castaneum* placed on them after three days and 68 per cent. after 21 days; the greatest kill recorded on any of the other eight control plates was 2 per cent. The waxed surfaces kept at 43°C. over DDT had acquired DDT vapour in such a way as to produce an insecticidal surface This might have come about through unequal heating of the desiccator causing DDT to evaporate from the reservoir at the bottom and condense on the plates, or it might be due to active absorption of the DDT vapour by the wax. The latter seemed the more probable explanation, since no increased toxicity was found on the plain glass surfaces kept at 43°C. It was concluded from this experiment that loss of DDT from glass plates occurring during storage in the dark at 43°C. was due to volatilisation, as the loss could be reduced by confining the plates in a desiccator over DDT. DDT is evidently sufficiently volatile at this temperature to produce insecticidal activity in a wax-coated plate confined over it for 21 days.

TABLE V.

Effect on toxicity of storing DDT-treated glass plates, both plain and coated with cabbage wax, at 43°C. in a desiccator over DDT. Kills obtained on plates stored at 18°C. in a free atmosphere are included in the Table for comparison.

	Percentage kill									
	Glass at 18°C.			Glass at 43°C.		Wax at 18°C.			Wax at 43°C.	
Days	0	3	21	3	21	0	3	21	3	21
% Concentrations of DDT										
0·18	100	100	100	100	100	100	100	100	100	100
0·1	97	100	100	100	90	100	100	100	100	100
0·056	97	100	76	88	13	100	100	97	97	100
0·032	76	64	50	58	21	85	97	79	91	64
0·018	44	30	3	15	0	3	58	6	24	70
0·01	12	12	18	3	3	13	14	9	19	42
0·0056	18	0	16	0	0	0	3	0	44	91
Control (no DDT)	0	1	0	2	0	0	0	1	14	68

Toxicity of DDT dissolved in Cabbage Wax.

The degree of toxicity associated with a known amount of DDT acquired from the vapour phase by plates coated with cabbage wax was measured. The coated plates were placed in a desiccator over solid DDT and maintained at 43°C. for periods of 1, 3, 6, 11 and 20 days. Six plates were exposed for each period of time. Four of these plates were analysed chemically, and the toxicity to *T. castaneum* of the other two was estimated by the technique already described, using glass surfaces freshly sprayed with a suspension of DDT crystals for comparison. The results are summarised in Table VI. The figures in column three of the Table give the calculated values of the kill that would be given by equal weights of DDT as crystals 50 μ in size, and were obtained by reading off the figures of column two on the probit line obtained from the comparison plates.

The kill and DDT content increased steadily up to 11 days' exposure but there was a falling-off of both at 20 days. There was a considerable variation between replicates at any given exposure period and an insufficient number of plates to give a reliable estimate of the true mean may have been used. This variation may have been due to convection currents inside the desiccator, and the position of the plates relative to these, or to unavoidable differences in thickness and texture of the wax films. The kills produced by DDT associated with wax were about the same as the kills produced by the same amount of DDT as a crystalline deposit.

TABLE VI.

Toxicity of plates coated with cabbage wax, after exposure to DDT vapour at 43°C.

Period exposed to vapour (days)	DDT content of wax (microgm. per plate) (mean of 4 reps.)	Calculated kill (%)	Observed kill (%) (mean of 2 reps.)
0 (control)	—	—	2
1	0	0	0
3	14	6	0
6	24	16	28
11	54	46	55
20	45	38	23

Log (LD50 × 1,000) for crystalline suspension, in terms of per cent. concentration sprayed :—1·37 ± 0·09.

Penetration of the Wax Film by DDT Vapour.

DDT acquired from the vapour phase by wax-coated plates might be dissolved in the wax and evenly distributed through it by diffusion, or it might be adsorbed on the surface of the wax. It seemed likely that the DDT would have a greater contact activity if it were purely superficial than if it were dissolved, because though the bodies of the test insects are in contact with the surface of the wax, only their tarsal extremities appear to penetrate it.

To determine the toxicity of wax containing known quantities of dissolved DDT, various dosages of DDT were dissolved with the wax in a common solvent and the solution sprayed on to plates to produce wax layers in the way already described. There was no sign of crystallisation of the DDT, and it was assumed that it was evenly distributed in the wax. The toxicity to *T. castaneum* of these plates was compared with that of plates sprayed with similar dosages of a suspension of DDT crystals. Table VII shows the mortalities produced on plates by wax and DDT together, and the LD50 for the crystal suspension.

In fig. 1 mortality figures from Table VII produced by films of cabbage wax containing dissolved DDT, are compared with values from Table VI, produced by wax films which had been exposed to DDT vapour. As there is no significant difference in the LD50's for crystalline deposits given in Tables VI and VII there is no reason to suspect any change in insect resistance between the two

TABLE VII.

Toxicity of plates coated with cabbage wax containing DDT.

DDT present (microgm. per plate) Mean of 2 replicates	Kill (%) Mean of 2 replicates
0 (control)	2
30	11
60	65
127	96

Log (LD50 × 1,000) for crystalline suspension in terms of per cent. concentrations sprayed:—1·43 ± 0·03.

LD50's from dosage mortality curves of DDT crystals on glass plates and DDT dissolved in wax:—

Crystals:— 69 microgm. per plate.
Wax solution:—53 microgm. per plate.

experiments. The points representing DDT and wax sprayed together fall close to a straight line. The points representing DDT acquired from the vapour phase show a good deal of scatter, but they do not suggest that DDT associated with wax in this way is more toxic. It was therefore concluded that DDT diffuses throughout the wax layer, and is not confined to its surface.

It is unfortunate that the toxicity of DDT crystals deposited on a glass surface is fairly close to that of DDT dissolved in cabbage wax (see Table VII). The results are not directly comparable as the lines are not parallel, the line for DDT dissolved in wax being flatter than that for DDT crystals, but they are so close together that no great change in toxicity could be expected if crystals of DDT lying on the surface of a wax film were to become dissolved in the wax. Hence, the method of measuring contact toxicity used in this work is not capable of distinguishing between these two forms of DDT.

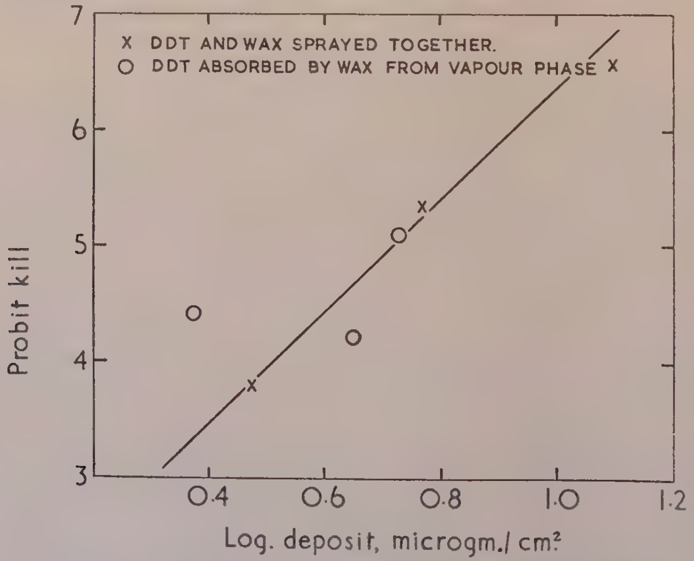


Fig. 1.—Toxicity of DDT dissolved in a film of cabbage wax 0·5 micron thick.

Solubility of DDT in Cabbage Wax at 43°C.

Plates were coated with an exactly known weight of wax, by running 0·35 ml. of a 1 per cent. solution of cabbage wax on to each plate, and allowing the solvent to evaporate. The plates were then heated to 70°C. in an oven for five minutes to remove traces of solvent. This procedure gave a thin but rather irregular film of wax on the plates. Each plate was covered with a layer of filter paper, on top of which was placed a second filter paper which had been impregnated with a large excess of DDT. On top of this was placed another glass plate. Thus, DDT vapour could diffuse through the lower filter paper and reach the wax layer. Several plates were prepared in this way, and placed in an oven at 43°C. They were withdrawn at intervals and analysed for DDT. The amounts of DDT found in the wax layer are shown in fig. 2. The maximum concentration of DDT in the wax was about 1·7 per cent. after 46 hours' heating.

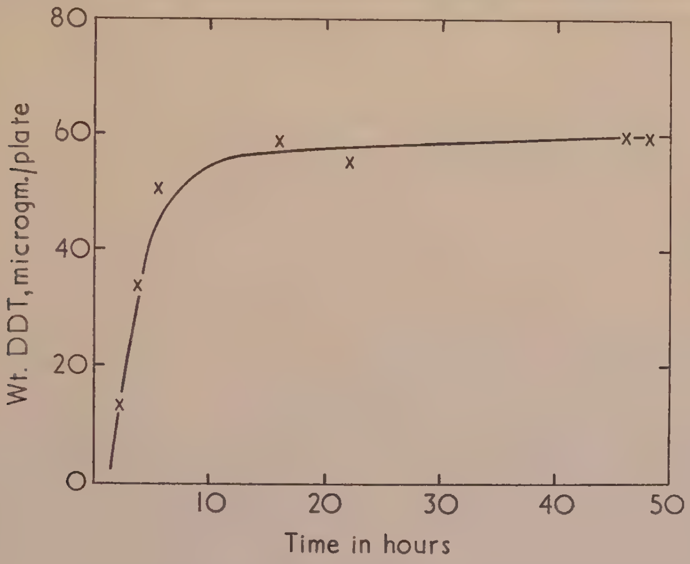


Fig. 2.—Weight of DDT picked up at 43°C. by cabbage wax applied to glass plates, each separated from a DDT-treated surface by a filter paper; 3·5 mg. of wax was applied to each plate.

Use of Ultra-violet Light to distinguish between Crystalline and Dissolved DDT.

The ready volatility of DDT at 43°C. suggested that when crystalline deposits on wax-coated plates were stored at this temperature, the part of the DDT which had not evaporated might have become dissolved in the film of wax. It has been reported (Wichman & others, 1946) that DDT in solution is readily decomposed by ultra-violet light, while crystalline DDT is resistant to it. If this is true of DDT solutions in wax, it provides a means of distinguishing between crystalline and dissolved DDT, or, where the two forms occur together, of forming an estimate of the proportion of DDT in solution. For if, of two identical plates, one is exposed to ultra-violet light and both are then analysed, the amount of DDT in solution in the wax can be calculated from the results of the two analyses.

Glass plates, both plain and coated with cabbage wax, were accordingly sprayed with DDT suspensions of various concentrations, determinations of deposit densities made immediately on samples of each, and the rest stored at 18°C. and 43°C. for periods of 5 and 14 days. A pair of plates was used for each treatment and one of each pair was then exposed for 30 minutes at a distance of 6 in. from an ultra-violet lamp of the type giving a high proportion of radiation at a wave-length of 2537 Å.U. A preliminary experiment had shown that under these conditions a plate with a deposit of 0·34 microgrammes of DDT per sq. cm., applied with the wax in solution in toluene, lost 95 per cent. of its DDT as shown by chemical analysis, while a plate with a crystalline deposit of about 1 microgm. per sq. cm. lost only about 30 per cent. of its DDT. This difference may be due to a greater sensitivity of the DDT when it is in solution. Alternatively, it may be due to the greater area exposed to the action of the radiation; for a crystalline deposit of this density covers only a very small proportion of the area of the plate. In either case it should be possible to use this effect as a means of deciding whether an appreciable proportion of a DDT deposit is dissolved in the wax. The solubility of DDT in the wax, even at 43°C., being only 1·7 per cent., it would be necessary, if any appreciable proportion of a DDT crystal is to dissolve in the wax layer (which is somewhat thinner than the crystal itself), for the dissolved DDT to diffuse away from the crystal in the plane of the wax layer, and in this way to expose a larger surface to the ultra-violet irradiation. It may therefore be concluded that if a deposit of DDT on a wax-coated plate, after suitable storage, is no more rapidly destroyed by ultra-violet light than a similar deposit on a plain glass plate, then only a negligible proportion of the DDT can be in solution in the wax. The results of chemical analysis of the plates, with and without exposure to ultra-violet light, are given in Table VIII.

TABLE VIII.

Effect of ultra-violet radiation on deposits of DDT on glass plates, both plain and coated with cabbage wax.

Treatment of plates	Original deposit (microgm./sq. cm.)	DDT deposit before exposure to U.V. (microgm./sq. cm.)		Per cent. of deposit remaining after exposure to U.V.	
		Glass	Wax	Glass	Wax
Stored 5 days at 43°C.	4	3·86	3·71	93	89
	7·2	5·03	5·13	93	89
Stored 14 days at 43°C.	2·2	0·01	0·04	Nil	Nil
	4	0·25	0·25	80	70
	7·2	3·35	4·36	71	76
Stored 5 days at 18°C.	0·4	0·43	0·47	63	45
	1·3	1·11	0·93	82	87
Stored 14 days at 18°C.	0·7	0·56	0·73	60	45
	1·3	1·11	1·30	92	72
Mean				70	64

The deposits on the duplicate plates are known to vary with a standard error of 5 per cent. to 10 per cent., so that it is impossible to know with any great accuracy the rate of deposit before exposure to ultra-violet radiation. The individual figures for percentage of deposit remaining after exposure are therefore not very reliable. The mean results, however, show that losses from the deposits on wax are not much greater than those from deposits on glass, so that if any of the DDT becomes dissolved in the wax, it is never, under the conditions of the experiment, more than a small proportion of the whole.

Discussion.

It has been shown that a deposit of DDT crystals resting on a film of plant wax is not appreciably dissolved by the wax except at a high temperature in a closed container; and that when solution in the wax does occur, contact toxicity to adult *T. castaneum* is not lost under the conditions of the test. Any solution of DDT by the wax that occurred under the conditions of these experiments might be increased if a smaller particle-size of the insecticide were used. But although the crystals used were approximately 50 μ long, they were only about 1 μ in diameter and hence they had a large specific surface, which would be the controlling factor in processes involving evaporation or diffusion; to study particles with a larger specific surface might be too great a departure from possible practical conditions. Should there be plant waxes in which DDT is more readily soluble, their effect on the persistence of the deposit might be greater, for not only would solution occur more rapidly, but re-volatilisation of the dissolved DDT would be reduced, and the result might be either increased persistence due to this cause, or reduced persistence due to the decomposition by sunlight of the DDT dissolved in the wax. It would be as well, therefore, where great persistence is required on any species of plant, to study the properties of its leaf wax and the effect it might have on the insecticide. But, since most plants have a much thinner layer of wax than that present on cabbage leaves, which was simulated in this work, it is unlikely that this layer by itself can have much influence on the toxicity or persistence of this type of DDT formulation. It would seem however, that DDT is able to penetrate this, the first layer of the plant cuticle, and that if it could be removed rapidly enough from the inner surface of the wax layer, a steady penetration of DDT into the plant could occur.

The possibility of loss of DDT by volatilisation has been mentioned by some workers (Decker & others, 1950; Hoskins, 1949) and others have demonstrated that loss of toxicity of insecticides is associated with high temperatures (Burgess & Sweetman, 1949; Teotia & Dahm, 1950; Mistric & Gaines, 1953), but volatilisation has not before been shown to take place to the extent which we have found under conditions which could occur in the field. That volatilisation is the chief cause of the losses observed at 43°C. is shown by the great reduction in the rate of loss from DDT deposits on unwaxed plates when they are stored in a desiccator over crystalline DDT. The remaining loss might be due to slow decomposition, but it is too small to be of practical importance. It may simply have been due to the time taken to saturate the atmosphere in the desiccator.

Summary.

The persistence and toxicity of DDT crystals on thin layers of plant wax were studied. Deposits of crystalline DDT at rates of 2 to 8 microgm. per sq. cm. were applied to glass plates, plain or coated with a 0·5 μ layer of wax obtained from leaves of sisal or cabbage. The plates were stored for various periods at 18°C. and at 43°C. (representing ~~temperature~~ and tropical leaf-temperatures). DDT remaining after storage was estimated biologically by means of its contact action on adult *Tribolium castaneum* (Hbst.), and chemically by a modification of the Schechter-Haller method. At 18°C., there was no significant change in any of the deposits when estimated chemically. But biological estimation showed that, although the toxicity of the deposits on waxed plates was unchanged, that on glass plates was doubled after storage for eight days. The reason for this change was not discovered. At 43°C., the amount of DDT, estimated both chemically and biologically, diminished rapidly and was negligible after 26 days. The loss of toxicity at 43°C. was shown to be accompanied by loss of weight of the deposits. Loss at 43°C. from plain glass plates could be much reduced by storing them in an atmosphere saturated with DDT vapour. It appeared,

tempe

therefore, that loss of toxicity at the higher temperature was due to volatilisation of DDT and not to decomposition.

Plates coated with cabbage wax, stored at 43°C. in an atmosphere saturated with DDT vapour, absorbed the vapour rapidly up to a maximum of 1·7 per cent. of the weight of the wax. The plates were then toxic to *T. castaneum* crawling on them. DDT dissolved in the wax layer was found to be about as toxic as the same weight of DDT per sq. cm. in crystalline form on a glass surface. DDT dissolved in wax was found to be decomposed by short-wave ultra-violet radiation more rapidly than were DDT crystals. By irradiating deposits and then analysing them, it was shown that DDT crystals on wax surfaces, when stored for up to 14 days at 43°C. or 18°C., do not become dissolved in the wax to an appreciable extent, provided that the plates are stored in a ventilated container.

It is concluded that, although DDT can be taken up by a typical plant wax, this effect is unlikely to influence the toxicity of the deposit unless the DDT is able to penetrate further than the wax layer.

Acknowledgements.

This work was financed by a grant from the Colonial Insecticides Committee; we wish to thank the Committee for permission to publish this paper. We also express our thanks to Mr. C. B. Symes, O.B.E., the Officer-in-Charge, Colonial Insecticides Research, and to Dr. C. Potter, Head of the Department of Insecticides and Fungicides, Rothamsted Experimental Station, for their helpful advice and encouragement.

References.

Bliss, C. I. (1934). The method of probits.—Science, **79**, p. 38.

Brunson, M. H. & Koblitsky, L. (1953). Parathion, DDT and EPN deposits on peach foliage and fruit.—J. econ. Ent., **45**, p. 953.

Burgess, A. F. & Sweetman, H. L. (1949). The residual property of DDT as influenced by temperature and moisture.—J. econ. Ent., **42**, p. 420.

Chisholm, R. D., Nelson, R. H. & Fleck, E. E. (1949). The toxicity of DDT deposits as influenced by sunlight.—J. econ. Ent., **42**, p. 154.

Curtis, O. F. (1936). Transpiration and the cooling of leaves.—Amer. J. Bot., **23**, p. 7.

Curtis, O. F. (1938). Wallace and Clum, "Leaf Temperatures": a critical analysis with additional data.—Amer. J. Bot., **25**, p. 761.

Decker, G. C., Weinman, C. J. & Bann, J. M. (1950). A preliminary report on the rate of insecticide residue loss from treated plants.—J. econ. Ent., **43**, p. 919.

Downing, G. & Norton, L. B. (1951). Modification of Schechter method of estimating DDT residue.—Analyt. Chem., **23**, p. 1870.

Finney, D. J. (1947). Probit Analysis.—Cambridge, Univ. Pr.

Fleck, E. E. (1948). Residual action of organic insecticides.—Industr. Engng Chem., **40**, p. 706.

Fleck, E. E. (1949). The action of ultraviolet light on DDT.—J. Amer. chem. Soc., **71**, p. 1034.

Fogg, G. E. (1948*a*). The penetration of 3:5-dinitro-*o*-cresol into leaves.—Ann. appl. Biol., **35**, p. 315.

Fogg, G. E. (1948*b*). Leaf penetration of spray chemicals.—Chem. Prod., **11**, p. 58.

GAHAN, J. B., TRAVIS, B. V. & LINDQUIST, A. W. (1945). DDT as a residual-type spray to control disease-carrying mosquitoes: laboratory tests.—J. econ. Ent., **38**, p. 236.

GRIFFITHS jr., J. T. & STEARNS jr., C. R. (1949). The effects of airplane DDT applications on citrus groves in Florida.—J. agric. Res., **78**, p. 471.

GUNTHER, F. A., CARMAN, G. E. & ELLIOT, M. I. (1948). Inhibition of the field decomposition of DDT spray deposits on citrus; preliminary results.—J. econ. Ent., **41**, p. 895.

GUNTHER, F. A., LINDGREN, D. L., ELLIOT, M. I. & LADUE, J. P. (1946). Persistence of certain DDT deposits under field conditions.—J. econ. Ent., **39**, p. 624.

HADAWAY, A. B. & BARLOW, F. (1949). Further studies on the loss of insecticides by absorption into mud and vegetation.—Bull. ent. Res., **40**, p. 323.

HOPKINS, L., NORTON, L. B. & GYRISCO, G. G. (1952). Persistence of insecticide residues on forage crops.—J. econ. Ent., **45**, p. 213.

HOSKINS, W. M. (1949). Deposit and residue of recent insecticides resulting from various control practices in California.—J. econ. Ent., **42**, p. 966.

HUFFAKER, C. B. (1948). A technique for translocation of DDT in plants.—J. econ. Ent., **41**, p. 650.

KOZLOVA, E. N. & DVORTSOVA, E. I. (1952). Rendering plants toxic with organic insecticides. [*In Russian.*]—Dokl. vsesoyuz. Akad. sel.-khoz. Nauk Lenina, **17**, no. 4, p. 41.

LINDGREN, D. L. & BOYCE, A. M. (1944). Results with dichloro-diphenyl-trichloro-ethane in control of the California red scale.—J. econ. Ent., **37**, p. 123.

LINDQUIST, A. W., JONES, H. A. & MADDEN, A. H. (1946). DDT residual-type sprays as affected by light.—J. econ. Ent., **39**, p. 55.

MCINTOSH, A. H. (1947). Relation between particle size and shape of insecticidal suspensions and their contact toxicity. I.—Ann. appl. Biol., **34**, p. 586.

MISTRIC jr., W. J. & GAINES, J. C. (1953). Effect of wind and other factors on the toxicity of certain insecticides.—J. econ. Ent., **46**, p. 341.

MUNGER, F. (1948). Body-temperature measurements of the California red scale.—J. econ. Ent., **41**, p. 422.

PLUMMER jr., B. E. & CARTER, R. H. (1946). Translocation of DDT to potato tubers.—Bull. Maine agric. Exp. Sta., no. 442 (Rep. 1945–6), p. 140.

POTTER, C. (1952). An improved laboratory apparatus for applying direct sprays and surface films, with data on the electrostatic charge on atomized spray fluids.—Ann. appl. Biol., **39**, p. 1.

SLOAN, M. J., RAWLINS, W. A. & NORTON, L. B. (1951). Factors affecting the loss of DDT and parathion residues on lettuce.—J. econ. Ent., **44**, p. 701.

STAFFORD, E. M. & HINKLEY, H. S. (1946). DDT and related compounds for control of black scale on olives.—Circ. Calif. agric. Exp. Sta., no. 365, p. 91.

SYMES, C. B., HADAWAY, A. B., BARLOW, F. & GALLEY, W. (1948). Field experiments with DDT and benzene hexachloride against tsetse (*Glossina palpalis*).—Bull. ent. Res., **38**, p. 591.

TEOTIA, T. P. S. & DAHM, P. A. (1950). The effect of temperature, humidity and weathering on the residual toxicities to the house fly of five organic insecticides.—J. econ. Ent., **43**, p. 864.

WAGGONER, P. E. & SHAW, R. H. (1952). Temperature of potato and tomato leaves.—Plant Physiol., **27**, p. 710.

WALLACE, R. H. & CLUM, H. H. (1938). Leaf temperatures.—Amer. J. Bot., **25**, p. 83.

WICHMAN, H. J., PATTERSON, W. I., CLIFFORD, P. A., KLEIN, A. K. & CLABORN, H. V. (1946). Decomposition and volatility of DDT and some of its derivatives.—J. Ass. off. agric. Chem., Wash., **29**, p. 218.

THE EXTERMINATION OF THE TSETSE FLY, *GLOSSINA MORSITANS* WESTW., AT ABERCORN, NORTHERN RHODESIA.

By P. E. Glover, C. H. N. Jackson, A. G. Robertson
and W. E. F. Thomson.

Abercorn (Lat. 8°50′S., Long. 31°23′E., altitude 1,600 m.) lies near the southern end of Lake Tanganyika and a few miles from the border of Tanganyika Territory. Between the town and the Lake the altitude decreases, often rapidly, towards the north-west, until at Lake level it is only 750 m. Cascading into the Lake are several swift and permanent streams including the Lucheche and the Luanzua with its tributary the Mwambeshi.

Mean annual rainfall varies from about 1,270 mm. on the Chisungu escarpment (1,120 mm. at Abercorn) to only some 700 mm. at Mpulungu. A meteorological station at Nsizye village (fig. 1), rather below the upper limit of *Glossina morsitans* Westw., gave mean maxima 30·1°C. for September 1939/46 and mean minima 12·4°C. for June; at Mpulungu on the Lake the maxima were 2°, and the minima 3°, higher. Saturation deficit was highest in September and October and lowest in January and February.

Abercorn lies on rocks of the Katanga system, mainly a sedimentary series containing conglomerates, quartzites, shales and sandstones. Granite outcrops occur along the Lake coast north of the Kalambo river mouth and between Mpulungu and the mouth of the Lufu river 25 miles west of Mpulungu. Much of the soil is acid and deficient in calcium and phosphorus. The normal sequence is from red sandy or gravel soils on the higher ground to reddish or chocolate loams on the footslopes and then into heavy red, grey or black clays in the hollows (" dambos ") below. In many cases the type of soil is directly conditioned by the underlying rock.

Flora.

The vegetation of the area has been well described by B. D. Burtt (1942) and illustrated by photographs. The main vegetation types are deciduous *Brachystegia* woodland (including *Pseudoberlinia*, formerly called *Julbernardia*, *Isoberlinia*, *Berlinia* and *Brachystegia*), deciduous thicket, lakeshore vegetation, evergreen riverine and swamp forest (" msitu ") and the vegetation of the marshes or " dambos ". Of these only the first and the last are of any significance for the tsetse fly, *G. morsitans*.

The deciduous woodland is divisible into several sub-types. Thus *Brachystegia allenii* occurs from about Lake level to 1,000 m.; it is a small grey-green tree with rounded crown and affects rocky hills, commonly in association with *Monotes*, *Lannea*, *Diplorhynchus* and *Pterocarpus*. Such country is little favoured by *G. morsitans*. *Pseudoberlinia globiflora*, together with *Brachystegia spicaeformis* and several species of *Combretum* and *Terminalia*, is commonest from 1,000 to 1,400 m. and occurs in close association with most of the former concentration sites of *G. morsitans* in the area. The grass cover is thin, usually on poor exposed sandy soil. Scattered *G. morsitans* only were found in woodland of *Brachystegia bussei*, a hillside species with smooth bark, as also in mixed woodland of *Pseudoberlinia paniculata* and *Brachystegia spicaeformis*, growing on the footslopes of hills and escarpments at 1,200 to 1,500 m. with much *Uapaca*, *Combretum*, *Terminalia* and *Pterocarpus* and a medium grass growth on red soil. Mainly above the former altitude limit of *G. morsitans*, *Brachystegia floribunda* codominates with *B. spicaeformis* at 1,500 to 1,800 m. together with *Monotes*, *Protea* and *Parinari*, while on the tops of rocky hills and escarpments occurs the flat-topped, " feathery " leaved *Brachystegia tamarindoides*, in company with *Dissotis*, *Euphorbia* and low-growing *Vellozia*. This community also was generally above the reach of *G. morsitans*.

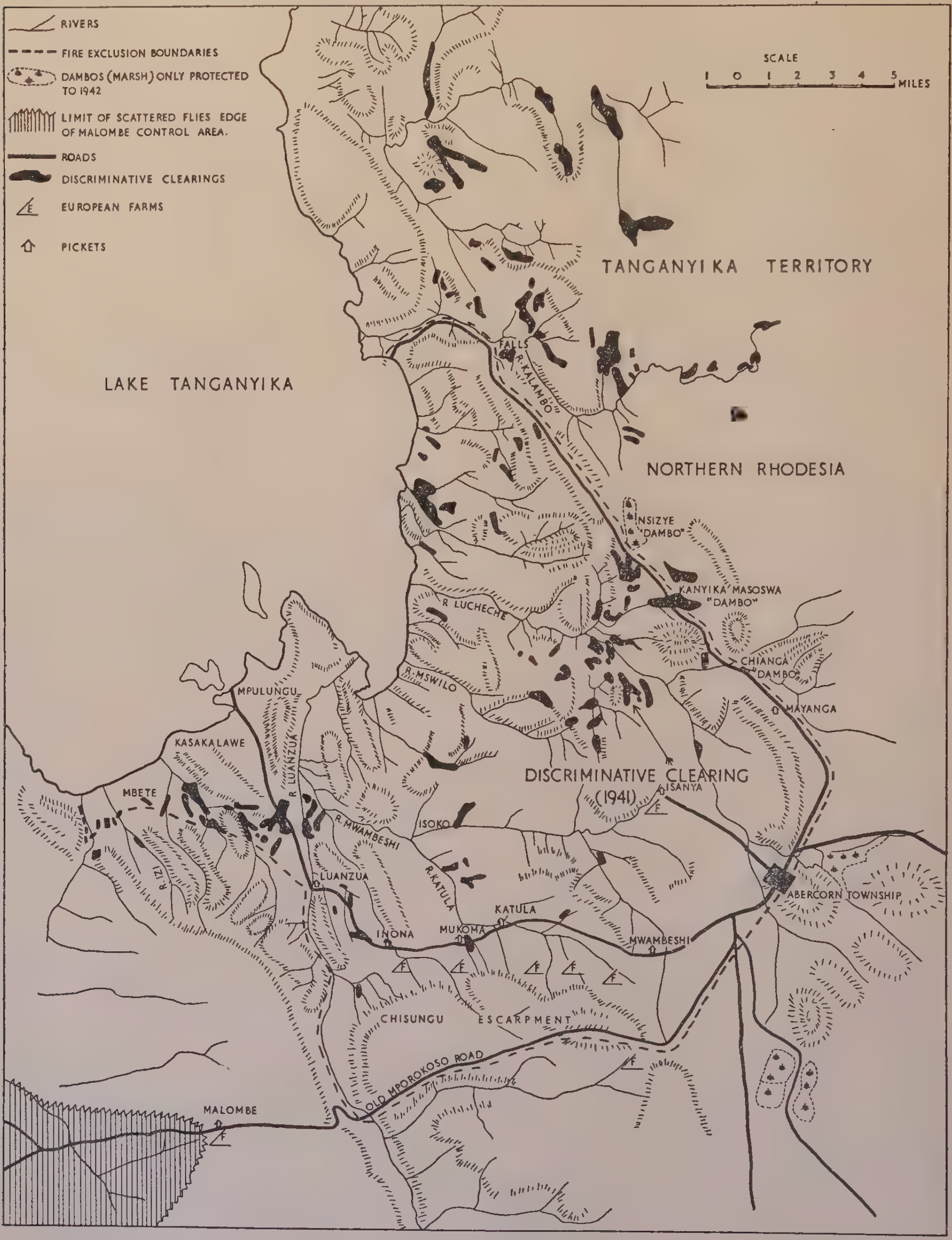

RIVERS
FIRE EXCLUSION BOUNDARIES
DAMBOS (MARSH) ONLY PROTECTED TO 1942
LIMIT OF SCATTERED FLIES EDGE OF MALOMBE CONTROL AREA.
ROADS
DISCRIMINATIVE CLEARINGS
EUROPEAN FARMS
PICKETS
SCALE
1 0 1 2 3 4 5 MILES
TANGANYIKA TERRITORY
LAKE TANGANYIKA
NORTHERN RHODESIA
FALLS
R. KALAMBO
NSIZYE "DAMBO"
KANYIKA MASOSWA "DAMBO"
CHIANGA DAMBO
MAYANGA
R. LUCHECHE
R. MSWILO
MPULUNGU
KASAKALAWE
R. LUANZUA
MBETE
R. IZI
R. MWAMBESHI
ISOKO
DISCRIMINATIVE CLEARING (1941)
ISANYA
R. KATULA
LUANZUA
KATULA
INONA
MUKOMA
MWAMBESHI
ABERCORN TOWNSHIP
CHISUNGU
ESCARPMENT
OLD MPOROKOSO ROAD
MALOMBE

Fig. 1.—Map of Abercorn, showing the area in which *Glossina morsitans* was exterminated.

Most of the marshes or dambos are perennial swamps in shallow valleys fed by permanent springs. They may be broad, green and trackless, or narrow glades winding into the distance. On the drier ground surrounding them a fringe of *Brachystegia taxifolia*, *Protea* and *Hymenocardia* may occur, and some dambos are studded with large-leaved *Terminalia* trees. There is a great wealth of flowers including yellow, orange and mauve ground orchids (*Eulophia*), *Kniphofia* ("red-hot pokers"), *Lasiosiphon*, *Coleus*, *Moraea* (wild tulip) and *Dissotis*. On the margins of some dambos large numbers of *G. morsitans* were to be found.

Fauna.

The Bovidae include roan antelope, *Hippotragus equinus*, fairly common and widespread; hartebeest, *Alcelaphus lichtensteini*, occasional; reedbuck, *Redunca arundinum*, common in the dambos; puku, *Adenota vardoni*, fairly common in Mbete area (fig. 1); waterbuck, *Kobus* sp., a few parties; duiker, *Sylvicapra grimmia*, common; blue duiker, *Philantomba caerulea*, fairly common in evergreen forest; grysbok, *Raphicerus sharpei*, fairly common; klipspringer, *Oreotragus oreotragus*, common on rocky hills in the Lucheche drainage; eland, *Taurotragus oryx*, a few parties; bushbuck, *Tragelaphus scriptus*, fairly common; and buffalo, *Syncerus caffer*, two herds, one of 37 animals shot out between 1942 and 1945, and the other unmolested.

Bushpig, *Potamochoerus porcus*, are very common and widespread but warthog, *Phacochoerus aethiopicus*, are not common. Hippopotamus, *H. amphibius*, were confined to the Lake shore. Elephant, *Loxodonta africana*, were irregular visitors up to 1944, since when they have become resident in the area.

Rock-rabbits, *Procavia*, are very common by the Lake shore and there are troops of baboons (*Papio*) and of monkeys (*Cercopithecus* and *Colobus*) in suitable localities.

Two migrant species of stork, *Sphenorhynchus abdimii* and *Ciconia ciconia*, were wont to appear in the Nsizye dambo area seasonally, sometimes in large numbers. The ground hornbill, *Bucorvus cafer*, was common.

About 1942, as an anti-rinderpest measure, some shooting of game animals took place north-east of the road from Abercorn to the Kalambo Falls (fig. 1), in the course of which the herd of 37 buffalo was exterminated, but otherwise there was no disturbance of the animals living west of that road.

The Attack on *Glossina morsitans*.

At the request of the Government of Northern Rhodesia, the late C. F. M. Swynnerton, C.M.G., Director, and the late B. D. Burtt, Botanist, Department of Tsetse Research, Tanganyika, visited Abercorn in 1935 and 1936 respectively. European farms then suffering from bovine trypanosomiasis transmitted by *G. morsitans* were mostly situated between the Chisungu escarpment and the road from Abercorn to its port at Mpulungu on Lake Tanganyika (fig. 1). Flies were scarce between the road and the escarpment, but they were numerous in the Mwambeshi valley below the road and in other sites between the Mwambeshi stream and Lake Tanganyika.

As a first measure of protection for the European farms, seven fly-pickets were established at the end of June 1936, to prevent carriage of flies upwards from the country between the farms and the Lake. These pickets (fig. 1) were called Luanzua, Inona, Mukoma, Katula, Mwambeshi, Isanya and Mayanga and they all remained in operation until the end of November 1949 except Mayanga which was given up in 1947 having caught no flies at all for over three years.

Complete fire exclusion was started in 1936 between the Old Mporokoso road above the Chisungu escarpment and the Mwambeshi river below the road (fig. 1), the other boundaries being the Lucheche and the Luanzua rivers. The area thus protected from fire was about 100 sq. miles. The ultimate object was to thicken the woody vegetation in order to make the country too dense for *G. morsitans*; a more immediate effect was, however, to keep certain swamps choked with long grass throughout the dry season, and this is believed to have rendered them unfavourable to the flies.

North of the Mwambeshi river, the country was to be burned early in the season in order, eventually, to achieve a similar densification of the woodland. By July of the following year the catches had fallen somewhat within the fire-excluded area, but not about Mswilo in the early burning area to the north of it, and the Isanya fly-picket, tapping the Mswilo area, was making large catches of *G. morsitans*. The fire-excluded area was therefore at once extended by a further 140 sq. miles as far as the road from Abercorn to the Kalambo Falls (fig. 1) before any grass fires had taken place. Later (1939–43) the three dambos on this road were also protected from fire, and finally, in 1940–41, a further 30 to 40 sq. miles was added between the Luanzua and Izi rivers (fig. 1), making a total of about 280 sq. miles, by which time the protected area was in contact with other fly-infested country on its north and north-east edges only.

Serious escape fires occurred from time to time in the protected area, notably in 1938 and 1941, when in each case about half the protected country was lost. Possibly for this reason, the reduction in numbers of *G. morsitans* at the fly-pickets was only about 35 per cent. over the first five years, and it was obvious that the action of the fire exclusion was extremely slow.

Generally low density of flies had hitherto hindered survey work, because when flies are very few several visits may be needed to confirm each site of apparently higher concentrations, but in 1941 an intensive survey by teams of 25 trained fly-boys, provided with bicycles and measuring wheels, located a number of recognisable concentrations of *G. morsitans* in a type of small valley known as " kasenga " in the Lungu language, of which the original example had been shown to us by a local guide the year before. This prototype kasenga, to quote the 1941 survey report, " starts between high hills as a narrow but flat-bottomed cleft a little under two miles long: after two miles it acquires a definite water-course and becomes a rocky ravine. The upper, flat-bottomed section supports a fair growth of trees, and the adjacent hillsides are also well wooded "—with *Brachystegia*: the trees in the valley were mainly *Terminalia* and *Combretum*. This flat-bottomed upper portion of the valley contained a concentration of *G. morsitans*, with apparent density of about 30 non-teneral males per 10,000 yards, a fairly high figure for Abercorn at that time.

Between 26th June and 12th August 1941 the trees in the valley and along the edge of the surrounding woodland were felled, and by the end of September several traverses showed no flies there at all. Furthermore, the apparent density of *G. morsitans* fell to a depth of a mile or more round about, where no clearing had been done.

This unexpectedly spectacular result led to the adoption of similar methods in other such situations, and to an intensification of the search for undiscovered concentration sites; most of the clearings were completed by the end of 1942, but a few more were done up to 1944. It is important to stress that, though the apparent concentration of flies in these upper drainages was fairly well marked, moderate and often only slightly lower densities were noted over much of the hilly woodland in between them, which being so much more extensive must have contained far more flies than did the concentration sites themselves, and it was therefore most surprising to observe the collapse of these woodland populations, which one might have supposed to be leading an existence independent of the often distant fly concentrations in the shallow valleys below.

Two types of valley were eventually recognised, and cleared of trees. The first was of the kasenga type already described and the second was distinguished by having steeper, stony sides and a sandy stream bed in the bottom, with frequently poorly grassed patches supporting the low-growing lithophyte *Vellozia* cf. *tomentosa*. Both types of valley were bordered by *Brachystegia* or more usually by *Pseudoberlinia globiflora* woodland, in which trees over 7½ m. high occurred at a density of two or three per 100 sq. m. Grasses in the woodland were *Loudetia*, *Eragrostis*, *Tristachya* and *Andropogon*; herbs such as *Commelina* could be locally abundant, while *Clematopsis*, *Scilla* and *Anthericum* occurred occasionally.

The soil was usually sandy and light yellowish-grey on the wooded slopes, but changed to brownish red or dark grey in the bottoms of the drainage lines, where it could be several feet deep though often tightly compacted or shallow where erosion had taken place as a result of recurrent cultivation. Where there was a deep soil in the drainage lines, clumps of grass such as *Hyparrhenia* up to 2 m. high might occur along the sides of the median watercourse, if any, but there were patches of shorter grass as well. Often the tallest grass was to be found along the sides of the drainage lines, while in the middle there was a poor cover and bare spaces appeared. Generally, the grasses in the drainage lines were of better quality than in the surrounding woodland. On stony and tightly compacted soil, *Sporobolus* and *Microchloa* were common short grasses, sometimes associated with sedges. *Terminalia sericea* and *Combretum* cf. *gueinzii* were the dominant trees, and most of the shrub and coppice growth was less than 1 m. high.

Besides felling the trees in the drainage lines themselves—a very light task because they were mostly small and few—we always extended the clearing through the ecotone into the margin of the pure *Brachystegia* or *Pseudoberlinia* woodland, but even so most clearings did not greatly exceed 100 m. in width. The felled trees were not cut up but were left lying *in situ* as a dense mass of interlacing branches on the ground. This was done partly to save work and partly because we supposed that the effect of the clearing might be made more immediate by discouraging game animals from walking freely up and down the valley.

The collapse of the fly community was observed by regular fly-rounds along the edge of the clearing, and if flies persisted for about six months the original clearing was extended where most flies were still being caught. Sometimes also it happened that new concentrations were formed nearby, and, though these might have proved to be temporary only, it was the practice to clear them as they were found in order to secure a speedier reduction of flies in the whole area.

During the period of our observations in Abercorn, regeneration in the clearing was of no importance, but, even in the absence of suitable habitats for them. we had to guard against infiltration of flies from the area north and east of the Abercorn-Kalambo road and from Tanganyika Territory beyond. Accordingly, clearings of drainage lines, without any fire exclusion, were pushed northward, to form a buffer zone, in an area of about 15 × 15 miles, occupying all the fly-infested country between Lake Tanganyika and the high ground to the eastward of it. This work was started in 1942 and completed in 1948, but two additional clearings in the Mbete area (fig. 1) were done as late as 1949 and 1950, respectively.

In the dry season of 1946 fire exclusion was abandoned within the whole experimental area, because it had seemed unnecessary to the success of the clearings extending into Tanganyika Territory to the north, and also because it was very unpopular with the local Africans living in the experimental area.

The clearings made in the experimental area totalled 2·2 per cent. of it, and the proportion cleared in the buffer area to the north was not greatly different.

In 1949 the Abercorn area was handed over as reclaimed country to the

Game and Tsetse Control Department of Northern Rhodesia for further observation.

Fly-catches within the Experimental Area.

The experimental area was reconnoitred in 1935 and 1936, and revisited in 1937, but it was not until 1938 that it became possible, from October, to station a whole-time Field Officer in charge of the observational work. Interruptions were then caused by the war, but two prolonged visits were made in 1941 by an officer with a large staff of Africans, and from October of that year a Field Officer was again in charge until 1947. After that time fully trained Africans continued routine observations under the general direction of the Tsetse Control Supervisor.

Thus, though our data for the first three years are sketchy, they are fairly complete from the time when the discriminative clearings were started in 1941, and many of the regular fly-rounds were kept up until 1953, when the report of the Tsetse Control Supervisor for May begins: " With the approval of the Director the usual Rounds have been discontinued owing to no fly having been caught on the Rounds for several years."

The Mswilo-Lucheche fly-round is a typical one. Before the first clearings the apparent density (number of non-teneral males per 10,000 yards) averaged about 50. The first clearings were done in August–September 1941, and for the years 1942 to 1946 the mean apparent density on this fly-round was 35, 15, 1·7, 0·1, 0·0. On the edge of the fire exclusion area, the Nsizye dambo was protected from fire from 1939 to 1943 inclusive, but the surrounding country north of the Kalambo road was not; an escape fire burned the dambo in 1941, and in 1942 discriminative clearings were made, not in the dambo, but in drainage lines above and below it. The mean apparent densities on the dambo margin for the years 1939–47 were: 248, 126, 323 (escape fire), 360, 34, 6, 0, 0, 1. At the Kanyika Masoswa dambo, which had no escape fire in 1941, the figures were: 63, 18, 25, 14, 11, 2, 0, 0, 0. Both sets of figures showed a rise in 1941, but it was more marked where the escape fire occurred. After the clearings, the abandonment of fire exclusion in these dambos failed to raise the catches there. That it did depress them to begin with is shown by the fall in the catch at the Mayanga picket (Table I, section 7) which tapped this area.

A characteristic of fire exclusion was that it did not in general show any immediate effect on the catches at the fly-pickets. Investigation showed that this was at least largely because, under fire exclusion, flies concentrated on paths, and on roads and firebreaks which in some cases (Katula and Isanya) led directly up to the pickets. These internal firebreaks were therefore abolished after 1941.

When the fire exclusion ceased in 1946, concentrations of flies appeared in places (especially in the Mbete area and about the Luanzua and Inona rivers) where they had not been detected before. The new concentration sites were cleared and the picket catches fell soon after.

Throughout the period 1949 to 1952 many of the old fly-rounds within the fire exclusion area were repeated monthly, with completely negative results. This seemed to leave no doubt that such very few flies as occurred in the area in these last years were brought in from outside, and that there was no breeding population of flies within it.

Meeting of the Sexes.

In 1942, when fly numbers had already been greatly reduced, an uninseminated though non-teneral female fly was captured in the Isoko area; such an observation had never before been made by the Tanganyika Department of Tsetse Research, who had invariably found that all wild females which had taken their first meal proved on dissection to be inseminated. (This dissection was first described by Mellanby, 1936.)

In the following year, 12 non-teneral females out of 136 (9 per cent.) were uninseminated; in 1944 the figure was 20 per cent. of 152 and in 1945 it was 29 per cent. of 42 dissected. A single non-teneral female caught between the Inona and Mukoma pickets near the Mpulungu road in 1948 was also virgin.

These findings strengthened our belief that there was later no breeding population of flies within the area, since even as early as 1942, when numbers were relatively high, the sexes were beginning to fail to encounter each other, and this effect increased yearly to 1945, after which numbers became extremely low and it seems certain that the great majority of females must then have remained virgin.

TABLE I.

Picket catches, July 1936 to June 1949.

Picket:	1	2	3	4	5	6	7		C
Year								Total	
Fire exclusion started									
1936–37	1,354	607	759	1,149	138	1,613	295	5,915	—
1937–38	1,668	472	660	889	276	2,655	390	7,010	—
1938–39	1,057	254	285	358	195	1,953	342	4,444	2,500
1939–40	1,447	378	355	683	308	3,033	269	6,473	3,493
1940–41	1,648	566	391	592	141	1,257	144	4,739	3,934
Discriminative clearing started									
1941–42	956	317	249	370	94	624	140	2,750	—
1942–43	281	132	150	205	30	154	32	984	—
1943–44	105	39	72	75	34	57	5	387	4,020
1944–45	20	9	22	24	11	21	0	107	4,060
1945–46	11	0	14	5	4	6	0	40	3,266
Fire exclusion abandoned									
1946–47	23	44	19	3	6	6	0	101	—
1947–48	21	28	17	7	5	4	—	82	—
1948–49	26	23	13	6	3	2	—	73	—

1, Luanzua; 2, Inona; 3, Mukoma; 4, Katula; 5, Mwambeshi; 6, Isanya; 7, Mayanga; and C, the Control Picket at Malombe (map).

From Table I it is apparent that flies continued to be caught in the experimental area until June 1949, and there was even some increase after fire exclusion was abandoned. The largest numbers were caught at the Luanzua and Inona pickets, those nearest to the Mbete area (fig. 1). In April 1950 four flies were caught in the Mbete area on a drainage line leading into the Musumbe stream, east and slightly north of the village of Kasakalawe. Further inspections revealed a few flies each time, and it was decided to clear the drainage line. The work was done in May, and a few flies were still being found near Kasakalawe in July, but in October and December no more were to be seen. In the last three months of 1950 no flies were caught at the Luanzua picket, and none at the Inona picket after March of that year.

It was therefore believed that with the destruction of this concentration site near Kasakalawe in May 1950 the last *G. morsitans* in the experimental area had been wiped out. In his Annual Report for the year 1952 the Director of Game and Tsetse Control, Lusaka, Northern Rhodesia, writes: " The fly position remained stable in the area freed by means of discriminative clearing by East African Tsetse and Trypanosomiasis Research and Reclamation Organisation and taken over by the Department in 1949."

Threat from the South-west.

The area of the former Abercorn fly-belt could conceivably be reinfested from the Lufu fly-belt above the escarpment to the south-west of it.

In 1946 some discriminative clearing was done west of Malombe (fig. 1) near the road, in a general area about ten miles by six, and it was supported by native cultivation in certain key sites up to 1952. In the three years 1944–46 a picket (not shown in fig. 1) at Howard's farm on this road took between 1,200 and 1,400 flies annually; from 1950 to 1952 inclusive the annual catches were 119, 21, 4. These discriminative clearings thus had a somewhat delayed action, but undoubtedly drove the Lufu fly-belt well away to the westward, and considerably lessened the danger of reinfestation of the Abercorn area from that side.

That there had been a danger was apparent from the catches at a picket (Upper Luanzua) placed where the Old Mporokoso road crosses the Luanzua river (fig. 1). This picket caught 62 flies in 1949 and 17 in 1950, and it was known that some foot passengers were eluding the pickets at Malombe and Howard's farm above the escarpment.

In 1950 the original Luanzua picket (fig. 1) was moved along the Mpulungu road to its junction with the road to Mbete. Here it caught 22 flies in 1950 (the last Mbete discriminative clearing being done in May), 4 in 1951 and 3 in 1952. The last five flies caught at this picket were all on men bringing fish from the very distant Lufu river, 25 miles away.

Threat from the North.

On the north the only barrier to reinfestation was the " buffer zone " (p. 61) of discriminative clearings sixteen miles deep, and extending across the Kalambo river into Tanganyika Territory. In his Annual Report, already quoted, for 1952 the Director of Game and Tsetse Control says: " Heavy concentrations in Tanganyika Territory north of the Kalambo River still present a danger, and four pickets were maintained to prevent the carriage of fly into Northern Rhodesia."

At Nsizye (fig. 1), where in 1938 a heavy and widespread concentration of flies had occurred, experimental cattle were introduced in 1943. There were occasional losses only up till early 1945, when a beast died with an infection of *Trypanosoma vivax.* All then remained well until 1948, but in October–December of that year there were three more deaths. The rest of the herd were then treated except one young bull which was overlooked and died in January 1949, after which all remained well until July, when they had to be moved as in that very dry year there was insufficient water at Nsizye to maintain them.

Nsizye is of course on the border of the buffer area and it was supposed that the deaths late in 1948 might have been caused by a single tsetse infiltrating from the north, possibly aided by mechanical transmission by other biting flies.

On the other hand, by 1948 cattle on the European farms between the Chisungu escarpment and the Abercorn-Mpulungu road had remained well for over three years and milch cows had been introduced without losses between the Luanzua river and the Mpulungu road, towards the Mwambeshi confluence. In June 1953 these milch cows were inspected by the Veterinary Officer and pronounced free from trypanosomiasis.

In April 1953 a report was received of a fly seen in the Isoko region, in the heart of the experimental area, and five days' reconnaissance there did then produce one fly. This it was supposed might also have infiltrated through the buffer zone beyond the Kalambo river.

As the Director of Game and Tsetse Control says, there is thus still a distinct danger of reinfestation from Tanganyika Territory, and continued vigilance is needed.

The Effect of Fire Exclusion.

Over very much of the area, even where, as in Isoko, no escape fires had ever occurred and the country had been preserved without fire from 1935 to 1946, there was no very obvious densification of the woodland. Counts showed that the total number of woody plants in the fire-excluded area was not greatly influenced by ten years' protection, for they averaged 4,626 per acre compared with 4,257 per acre outside. However, the fire-excluded areas examined did show a larger proportion of plants in the 3 to 12 ft. categories and a lower proportion in the categories 0 to 3 ft., and also grasses were less abundant in the fire-excluded area than outside it.

Opportunity was taken to examine one area on a farm that had been protected from fire for 18 years, and here it appeared that the physiognomy of the vegetation was changing; creeping and under-shrubs seemed to be more numerous and there was an impression that, given a sufficiently long period of protection from fire, this *Brachystegia* woodland might ultimately give way to evergreen forest.

As a short-term means of reducing the numbers of *G. morsitans*, however, it appeared that fire exclusion could not be very effective through increasing the number of woody plants in the *Brachystegia* woodlands, for the general effect was to permit the upgrowth of very stunted individuals (0 to 3 ft.) to produce only a two to three times increase in plants from 3 to 12 ft. high, and this process took ten years. Any fairly immediate effect that there may have been must, therefore, be ascribed directly to the presence of unburned grass throughout the year.

That there was a real effect on fly numbers cannot be doubted. Thus, for example, the catches of flies in the dry season months June to October at the Mukoma and Katula pickets (tapping the unburned Isoko area, see fig. 1) totalled 1,234. 872, 444, 582 and 514 for the five successive years 1936–40. Similarly, on the Mswilo fly-round (burnt out in 1938) the mean numbers of non-teneral males per 10,000 yards for April–September, 1939 to 1941, were 19, 9, 4. This was before any discriminative clearing had been done in the Mswilo neighbourhood. The effect, though definite, was however slow.

The Effect of the Discriminative Clearings.

These were unexpectedly successful, in that their effects were not merely local but widespread, and they acted very much more quickly than fire exclusion. They also proved effective outside the fire-exclusion area.

How the clearings acted has been the subject of considerable debate. Some think that the valleys selected for clearing had been the mating grounds of the sexes and that when deprived of them the flies failed to meet. The natural supposition that they were feeding grounds cannot be supported by any evidence, for in fact the flies caught in them were well fed; however, this cannot be taken as really contrary evidence, for the valleys were so narrow for the most part that the catchers trying to sample them would inevitably attract some flies from the bordering woodlands.

It must be confessed that we do not know what vital rôle these valleys played in the ecology of the flies; we only know that cutting down the trees in and immediately around them put them out of action.

Summary.

European farms at Abercorn had been suffering from bovine trypanosomiasis carried by *Glossina morsitans* Westw., and the Tanganyika Department of Tsetse Research were asked in 1935 to advise.

Fly-pickets were established in 1936 to prevent carriage of flies on to the farms, and a belt of country was protected from fire, with the object of thickening the woody vegetation so as to make it unfavourable to *G. morsitans*. The fire-protected area was extended and continued until 1946; serious escape fires occurred in 1938 and 1941. During these first five years the reduction in catches at the pickets was only about one-third.

An intensive survey of the area was made in 1941, as the result of which concentrations of flies were identified in certain shallow valleys forming the headwaters of small tributary streams. Several of these were cleared of trees, with the result that the apparent density of *G. morsitans* was at once depressed not only in the valleys themselves but over wide areas of untouched woodland round about.

In 1942 and the following years these clearings were extended to new valley sites as they were discovered, both inside and outside the fire-excluded area, and always with striking effects. The last clearing of all was done in 1952.

From 1942 an increasing proportion of female *G. morsitans* remained virgin through failure of the sexes to meet, and by 1945, 29 per cent. of non-teneral females had not been inseminated. The proportion doubtless increased thereafter, and there can have been no breeding population of flies in the area for several years.

The general effect was seen in the fly-picket catches, but during the régime of fire exclusion these showed a considerable lag when compared with fly-rounds within the fly habitat itself, because the unburned grass caused the remaining flies to concentrate on paths and firebreaks along which they were carried to the pickets.

There was slight infiltration from the Lufu fly-belt to the south-west, which greatly diminished when the nearest portions of that belt were also attacked by discriminative clearing in 1946. The Lufu flies are separated from the Abercorn belt by high country which forms a barrier across which flies are occasionally carried on men.

There was also slight infiltration of flies from Tanganyika Territory to the north, which was separated from the Abercorn belt only by a buffer zone of discriminative clearings to a depth of 16 miles. Cattle, however, can now be kept in the Abercorn area with negligible danger of trypanosomiasis.

Fire exclusion alone was not a quick means of reducing fly numbers. Discriminative clearing, with or without fire exclusion, was very effective and cheap. How it worked we still do not know.

The total area of the discriminative clearings was less than 3 per cent. of the whole experimental area of 280 sq. miles.

Acknowledgements.

A great many people contributed to the Abercorn experiment, which was initiated by a request for action by Misses Marian and Hope Gamwell of Abercorn. The preliminary inspection by the late C. F. M. Swynnerton in the dry season of 1935 and the longer wet season survey by the late B. D. Burtt in 1936 have already been mentioned. They were both accompanied by the Senior African Assistant of the Tanganyika Department of Tsetse Research, Mr. Swedi Abdalla, who also returned with other officers in later years, thus assuring the repetition

of comparable fly-catches in selected spots. Dr. C. H. N. Jackson visited the area in 1937, 1938, 1940 and 1941; Mr. A. G. Robertson was stationed there from 1938 to 1940, when he was relieved by Mr. W. E. F. Thomson for a short time, and Mr. Thomson returned there from late in 1941 to 1946. Dr. P. E. Glover made a botanical investigation of the effect of fire exclusion late in 1948. Mr. S. Napier Bax guided the work from 1938 to 1948 and paid a number of visits to the area; it was through his initiative that the intensive and successful survey of 1941 was carried out. Several local residents of Abercorn took over the task of fire control from time to time, and latterly Mr. J. H. Venning assumed the task of general supervision of all the work, from 1946 until the present time. In 1949, as already mentioned, Mr. T. Vaughan-Jones of the Northern Rhodesia Department of Game and Tsetse Control took over the direction of the work.

References.

Burtt, B. D. (1942). Some East African vegetation communities.—J. Ecol., **30,** pp. 65–146.

Mellanby, K. (1936). Experimental work with the tsetse-fly, *Glossina palpalis*, in Uganda.—Bull. ent. Res., **27,** pp. 611–632.

Northern Rhodesia. Game & Tsetse Control Department. (1953). Annual report for the year 1952. Lusaka.

THE MOSQUITOS (DIPTERA: CULICIDAE) OF THE SEYCHELLES.

By P. F. Mattingly
British Museum (Natural History)
and
E. S. Brown
Commonwealth Institute of Entomology.

(Plates I–III.)

The material on which this paper is based was collected by one of us (E.S.B.) whilst on secondment to the Seychelles Government from January 1952 to April 1953. The first author (P.F.M.) is responsible for the sections dealing with taxonomy and zoogeography and for the two appendices covering the mosquitos of other islands in the western Indian Ocean and proposed corrections to the key to larvae of *Culex* (Hopkins, 1952). The second author (E.S.B.) has contributed the section on bionomics and local distribution.

The first mosquito to be recorded from the Seychelles was *Aëdes aegypti* (L.) from Port Victoria, published by Theobald (1903). The same author (1912) added a further eight species in his report on the material brought back by the Percy Sladen Trust Expedition of 1905. One of these was, however, recorded only from Aldabra, which is not included in the Seychelles group as here defined. At the time of publication of the third volume of " Mosquitoes of the Ethiopian Region " (Edwards, 1941) no further species had been added, except for *Anopheles gambiae* Giles, again from Aldabra only (Hermitte, 1931). On this occasion Edwards gave it as his opinion that the collections so far made were " probably fairly complete ". Nevertheless a visit to the islands a few years later yielded no fewer than three additional species, one of them endemic, despite the fact that collecting was largely restricted to the immediate neighbourhood of Port Victoria (Harper, 1947). A further collection by E.S.B. is described here for the first time. It is interesting to note that, despite fairly thorough collecting and the presence in his material of a new endemic species and a new subspecies, Brown failed to find two of the species brought back by the Percy Sladen Expedition, one of which was also found by Harper. Thus none of the collectors who have visited these islands has failed to add at least two species or subspecies to the faunal list and none has succeeded in bringing back all the species known to occur. There is thus good reason to hope that future collectors will reveal additional elements in the mosquito fauna while at the same time discovering the early stages of the very interesting endemic species for which these are still unknown. It seems likely that the plant-axil fauna, in particular, has not as yet been fully explored and those plants so far neglected may well yield new species. In this connection the discovery by Doucet (1950, 1951*a*, *b*), in Madagascar, of a group of species related to *Ficalbia* (*Etorleptiomyia*) but placed by him in a new genus, *Ravenalites*, is worth special mention. This group was first found in leaf axils of *Ravenala* but has since been found also in *Pandanus* and an araceous plant of the genus *Typhonodorum*. The genus *Harpagomyia* is another which breeds exclusively in plant axils and Hopkins (1952) has suggested that the unknown early stages of the endemic Seychelles species *Culex scotti* Theo. are likely to be found in breeding places of this kind.

The provisional faunal list which follows is based on the collections enumerated above. A number of names have been omitted for reasons given below.

1. *Uranotaenia pandani* (Theo.)
2. *Uranotaenia nepenthes* (Theo.)
3. *Uranotaenia browni*, sp. n.
4. *Taeniorhynchus* (*Mansonioides*) *uniformis* (Theo.)
5. *Aëdes* (*Ochlerotatus*) *vigilax* ssp. *vansomerenae*, ssp. n.
6. *Aëdes* (*Stegomyia*) *aegypti* (L.)
7. *Aëdes* (*Stegomyia*) *albopictus* (Skuse)
8. *Aëdes* (*Aëdimorphus*) *albocephalus* (Theo.)
9. *Aëdes* (*Skusea*) *pembaensis* Theo.
10. *Culex* (*Neoculex*) *stellatus* van Someren
11. *Culex* (*Culex*) *simpsoni* Theo.
12. *Culex* (*Culex*) *pipiens* ssp. *fatigans* Wied.
13. *Culex* (*Culex*) *scotti* Theo.

Two names used by Theobald (1912) have been abandoned. These are *Stegomyia scutellaris* (Wlk.), which clearly represented a misdetermination of *Aëdes albopictus*, and *Reedomyia seychellensis* Theo., tentatively sunk by Edwards (1941) as a synonym of *Aëdes albocephalus*. The name *Culex antennatus*, listed by Harper (1947), was clearly a *lapsus calami* for *Culex scotti*. The name of *Aëdes fryeri* (Theo.), included in the Seychelles list by Edwards (1941) and Harper (1947) on the basis of its occurrence on Cosmoledo I. and by Theobald (1912) on the basis of its occurrence on Aldabra, is omitted for geographical reasons as noted above. This species and others occurring on islands in the western Indian Ocean other than the Seychelles proper are discussed in an appendix to the present paper. The name *Aëdes rhecter* Dyar was tentatively proposed by Edwards (1932) in the synonymy of *Reedomyia seychellensis* but may now be discounted as may the name *Ochlerotatus nigeriensis* (Theo.) applied by Edwards (1912) to *Aëdes fryeri*. The "*Taeniorhynchus* species?" of Theobald (1912) is here tentatively assumed to have been *T. uniformis*. The name *Uranotaenia nepenthes* was temporarily sunk by Edwards (1932) as a synonym of *U. pandani* but was re-established by him, without any doubt correctly, in 1941.

TAXONOMY.

Uranotaenia pandani (Theo.).

Adult male.

The male terminalia have been rather inadequately described and figured by Theobald (1912) and Edwards (1941). Since they are apparently indistinguishable

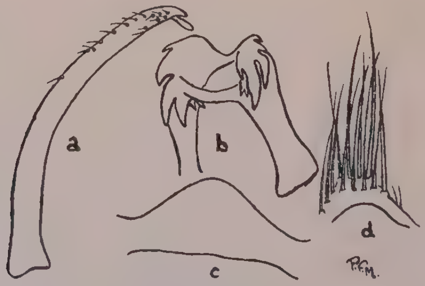


Fig. 1.—*Uranotaenia pandani.* Male terminalia showing: *a*, style; *b*, phallosome; *c*, IXth tergite; *d*, basal lobe of coxite.

from those of *U. nepenthes* and the new species described below, the following description and figure (fig. 1) will serve for all.

Style long, relatively slender, tapering with well developed terminal appendage and numerous microsetae on the distal half. Basal lobe of coxite strongly developed with numerous bristles of which one is conspicuously longer and somewhat stouter than the rest. IXth tergite smooth, rounded, convex. Phallosome with a number of recurved teeth.

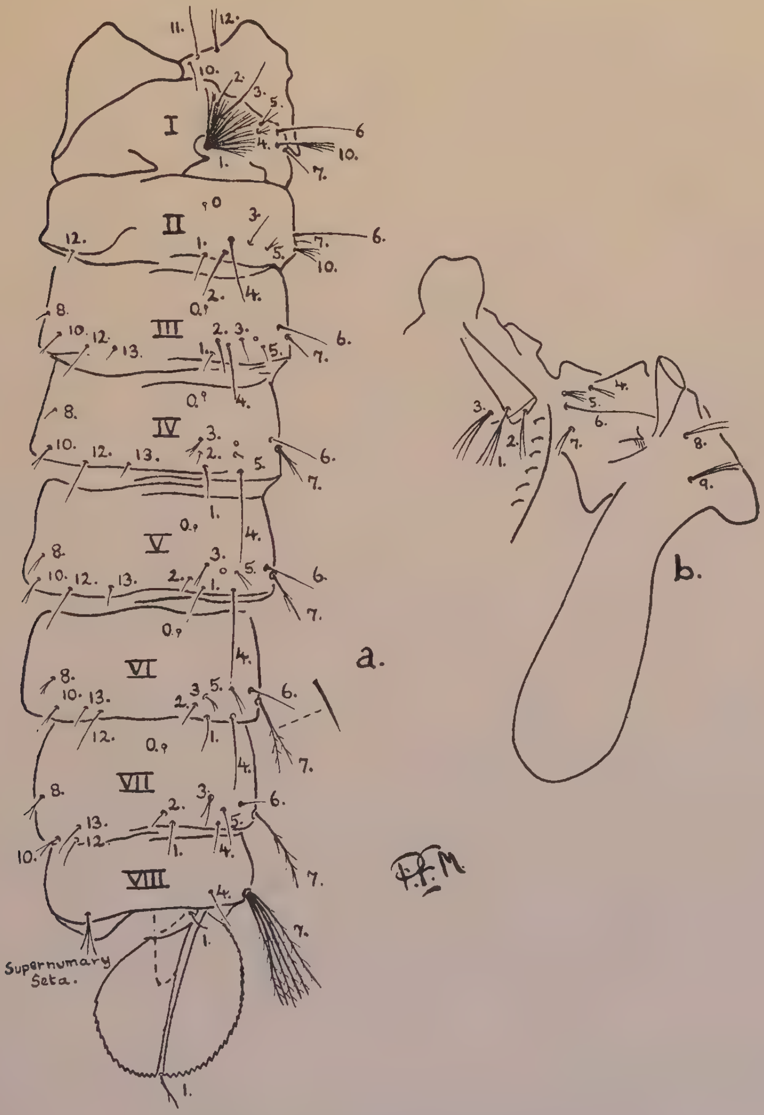


Fig. 2.—*Uranotaenia pandani*. Pupa: *a*, metanotum and abdomen; *b*, cephalothorax. Dorsal abdominal setae on the right, ventral abdominal setae on the left.

Pupa.

This has not previously been described. The description and figure (fig. 2) which follow are based on two pelts from Mahé I. and Cerf I. respectively, with associated adults, in the British Museum. The setal nomenclature employed is that of Belkin (1952, 1953*a*). Belkin (1953*b*, 1954) has suggested certain alterations to this nomenclature. At the time of writing, these two papers were in the press. Professor Belkin very kindly sent copies of his manuscripts, but these were not received until the descriptions and figures in the present paper had been completed. The necessary amendments are not difficult to make.

Trumpets short, broad at the apex, tapering sharply to the base, distal aperture an elongated oval flattened at one end, meatus about seven-tenths of the greatest length. *Cephalothorax*, setae 1 and 3 short, trifid, 2 and 4 short, single or bifid, 5 short, trifid or tetrafid, 6 long, stout, single, 7 short, bifid, 8 short, single or bifid, 9 short, trifid. *Metanotum* with 10 short, single or bifid, 11 short, single, 12 short with 2–4 branches. *Abdomen.*—Segment I with 1 very large, forming a conspicuous tuft with about 5–8 primary branches and numerous lightly plumose secondary branches, 2 and 3 single, 3 about twice as long as 2, 4 and 5 minute with 2–4 branches, 6 long and single, 7 minute and single, 10 short with about 4–6 branches. Segment II with 0 minute, single, 1 short, single or bifid, spinelike, 2, 3 and 4 short, single, 2 and 4 spinelike, 5 minute, bifid or trifid, 6 long, single, 7 minute, single, 8 not seen, 10 short with 2–5 branches, 12 minute, single. Segment III with 0 minute, single, 1 minute, single, 2 and 4 single, spinelike, 4 about twice as long as 2, 3 short, single or bifid, 5 minute with about 1–3 branches, directly posterior to or somewhat outside the hairless setal ring, 6 short, single, 7 short, single, spinelike, 8 short, single or bifid, 10 short, bifid, 12 short, single or bifid, 13 minute, single. Segment IV with 0 minute, single, 1 short, single, 2 minute, single, 3 short, bifid or trifid, 4 stout, single, 5 short, bifid or trifid, just posterior to or just inside or outside the hairless setal ring, 6 short, single, 7 stout, spinelike, plumose or simple, 8 minute, single or bifid, 10 minute, bifid, 12 short, single, 13 minute, single. Segment V with 0 minute, single, 1 short, single, 2 minute, single, 3 short, bifid, 4 long, stout, single, 5 minute, bifid or trifid, just posterior to or just outside the hairless setal ring, 6 short, single, 7 stout, spinelike, plumose or simple, 8 minute, single to trifid, 10 minute, bifid to tetrafid, 12 short, single or bifid, 13 minute, single. Segment VI with 0 minute, single, 1, 2 and 3 short, 1 single, 2 and 3 single or bifid, 4 long, stout, single, 5 minute, single or bifid, 6 short, single, 7 stout, spinelike, single or bifid, plumose or simple, 8 minute, bifid or trifid, 10 minute, bifid or trifid, 12 short, single, 13 minute, single. Segment VII with 0 minute, single, 1 and 2 minute, single, 3, 4 and 5 short, single or bifid, 6 minute, single, 7 stout, single to trifid, plumose, 8 short, bifid, 10 minute, single or bifid, 12 and 13 short, single. Segment VIII with 0 minute, single, 1 short, stout, single, 4 short, single or bifid, 7 stout, plumose, with 5–6 branches. The Cerf I. pelt has a short additional seta immediately ventral to 4. This is bifid on one side and trifid on the other. *Paddles* broad and blunt-ended, the distal tip emarginate. Seta 1 split or with light plumose branching at tip, 2 not seen. Fringe of short, stout, sharp spines extending from base of outer edge to about half way between seta 1 and the base of the inner edge.

Larva.

This has been described and figured by Mrs. van Someren in Hopkins (1952). She did not, however, describe or figure the mentum or figure the head (fig. 3). The homologies of the head setae seem to be particularly obscure in this group. It has therefore been thought preferable to adopt the relatively noncommital nomenclature of Hopkins (1952) rather than that of Belkin (1950).

The following additional details of variation are based on a large collection of larvae, made by E.S.B., from all the localities listed below under Distribution. Head seta A occasionally bifid. Mentum with 8 teeth on either side of the main central tooth. Comb with 5–10 spines. Pecten with 2–5. Subventral tuft of siphon with 2–4 branches. Proximal seta of ventral brush also with 2–4. Apart from this the agreement with the larvae described by Mrs. van Someren is very close. Through the kindness of Dr. Paulian of the Institut Scientifique de Madagascar I have been able to examine a larva of *U. pauliani* Doucet (1949*b*) and I am now satisfied that this is a synonym of *U. pandani*. In particular, the pecten teeth and antennal seta appear to be identical (see discussion in Hopkins, 1952).

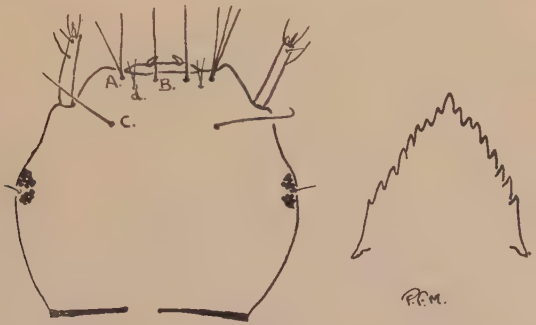


Fig. 3.—*Uranotaenia pandani*. Larval head and mentum.

Uranotaenia nepenthes (Theo.).

Adult male.

The male terminalia have not previously been described. They are apparently identical with those of *U. pandani*.

Pupa (fig. 4).

This has not previously been described. The present collection contains three pelts from Silhouette I. with associated adults. They show the following differences from *U. pandani* as described above.

Cephalothorax with setae 1 and 2 single or bifid, dark and rather stout, 3 single, 4 and 5 short, single, dark and rather spinelike, 6 single or bifid, dark and very stout, 8 and 9, short, dark, unbranched. *Abdomen* with seta 1 on segment I greatly reduced. Seta 6 on segments I and II and seta 7 on remaining segments extremely stout and dark, 7 single on segment III, single or bifid on IV–VII and bifid to tetrafid on VIII. Seta 4 shorter on segments II and III, rather longer on segments IV and V, bifid in some cases on IV and V, otherwise single, very stout and dark on II–VI. Remaining setae showing a general tendency to be shorter, stouter and darker than in *U. pandani*, nearly all of them unbranched. Seta 7 is reduplicated on one side of segment V of one specimen, apparently an aberration. The paddles, although similar in shape, are markedly smaller.

Larva (fig. 5).

No associated pelts are available but the present collection contains numerous whole larvae from the same breeding places as bred-out adults. No other larvae were obtained from any pitchers and it seems virtually certain that they can be attributed to *U. nepenthes.* Nor can there be any doubt that this is the larva tentatively attributed to *U. nepenthes* by Theobald (1912) and Hopkins (1952). The description given by these authors is somewhat deficient owing to the fact that the head setae and pecten teeth are almost invisible in the balsam mounts with which they worked. In Hopkins (1952) I followed Edwards (1941) in suggesting that *U. nepenthes* might be a colour form of *U. pandani.* From the larval material now available it is clear that it is a distinct species. At the same time I tentatively synonymised it with *U. pauliani.* This is now considered to be a synonym of *U. pandani* (see above). Paulian (1950) has given a description and figure of the larva of Madagascan *U. nepenthes.* The larva which he describes differs from our topotypic larvae from Silhouette I. and may be that of another species. In so far as the differences apply to the head setae, however, they may be illusory since these are exceedingly difficult to see.

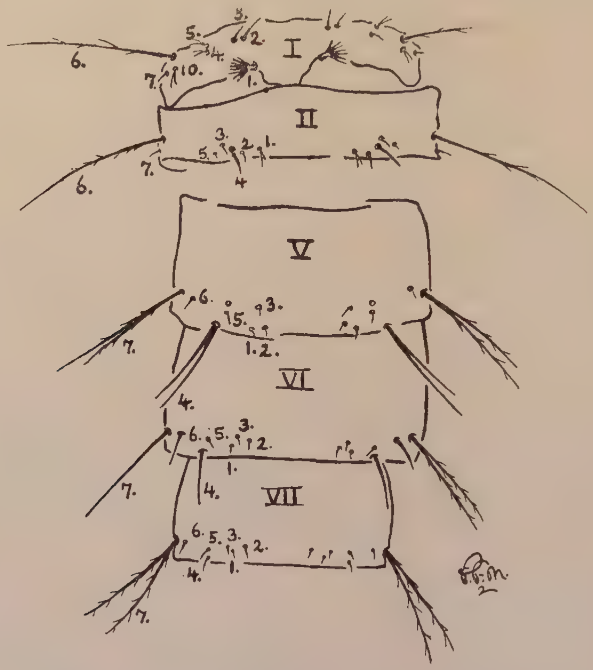
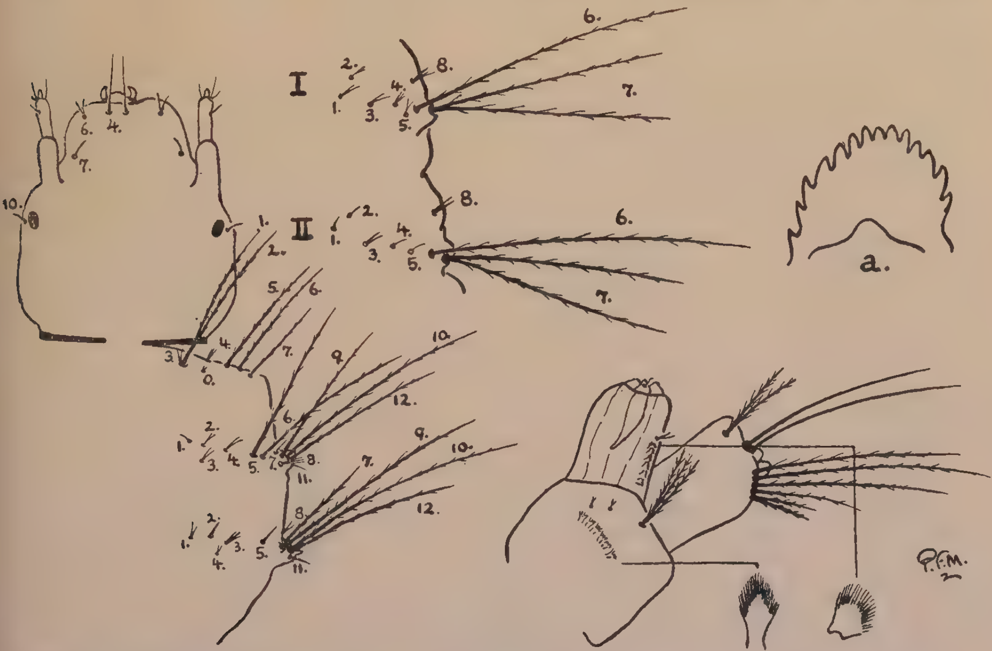


Fig. 4.—*Uranotaenia nepenthes.* Pupa: abdominal segments I, II and V–VII in dorsal view only.

The description which follows is based on four whole larvae from Morne Pot-à-Eau and one whole larva from Congoment, all from *Nepenthes* pitchers, collected by E.S.B. and on the five whole larvae from an unnamed locality above 2,000 ft. in the same area collected by the Percy Sladen Trust Expedition (Theobald, 1912; Hopkins, 1952). The figures in brackets indicate the nomenclature applied by Belkin (1950).

Head markedly narrower than in *U. pandani.* Antenna very short, smooth. Antennal seta minute, arising at about 7/10ths of the distance from base to apex, often difficult or impossible to see in whole mounts. Clypeal spines very short and stout, much as in *U. pandani.* Head seta A (7) minute, unbranched, B (6) minute, bifid, *d* (4) long, straight, moderately stout, simple, recalling the inner clypeal setae of *Anopheles.* Seta A (7) is very delicate and was overlooked by Theobald and Hopkins. Once its position had been established in chlorogum mounts, however, it proved quite easy to find even in Theobald's old balsam mounts. Mentum with the teeth larger than in *U. pandani* and only 6, or sometimes 7 on either side of the main central tooth. *Thorax* with the principal setae very long, stout and dark. *Abdomen* with lateral setae of first six segments long, stout and dark. Comb of 6–8 transparent, delicately fringed scales.



F'g. 5.—*Uranotaenia nepenthes.* Larva, showing head, thorax and first two abdominal segments, terminal segments of abdomen and labium (*a*). The setal nomenclature is that of Belkin (1950).

Siphon very short, approximately equal in length to the saddle, index about 1½ in crushed specimens. Pecten of 6–8 broad, very transparent, delicately fringed scales. Subventral tuft of two very short, stout, stiff, dark-coloured branches or, on one side in one larva, more delicate and trifid. Upper caudal seta single or double, lower single. Saddle hair single or bifid. Ventral brush comprising 5 pairs of stout plumose setae, unbranched except for the proximal pair which may be bifid. Anal papillae very small and rounded; the very strongly developed, stout, dark thoracic and abdominal setae are interesting. They are exhibited also by the Indomalayan *U. xanthomelaena* Edw. (1925) and *U. ascidiicola* de Meij. (1910), both of which also breed in pitcher plants. Quite a number of other species have long stout lateral setae on the thorax and first two abdominal segments but not on the posterior segments. The presence of these setae inclined Edwards (1941) to suspect that *U. nepenthes* might belong to an entirely different group from *U. pandani*. The discovery of the male, however, clearly shows their very close relationship. The hypothesis that such setae are adaptive to the larval habitat is discussed below under *Culex stellatus*.

Uranotaenia browni, sp. n.

The adult of this species closely resembles that of *U. pandani* from which it can, however, be readily distinguished by the absence of pale basal bands from the abdominal tergites. The pupa shows good distinguishing characters, particularly on segment VII of the abdomen and the larva here attributed, on the basis of unassociated material, is quite unlike that of any other species of *Uranotaenia* hitherto described. The following description of the adult is based on holotype ♂, allotype ♀, one paratype ♂ and two paratype ♀♀ bred out from fallen leaves of coco-de-mer in the Vallée de Mai, Praslin I. (*E. S. Brown*, 22.vi.1952). All these specimens are in the British Museum.

Adult male.

Head.—Proboscis long, dark, slender, distinctly wider at the tip than at the base but not very markedly so. Palps about 1/7th the length of the proboscis. Scales of vertex and occiput blackish. *Thorax.*—Mesonotum with integument mainly pale orange except to either side of the pre-scutellar bare patch where it is conspicuously darkened, rather sparsely covered with narrow, curved, black scales. Anterior pronotum yellowish, bare. Pleurae with integument pale yellowish, very much defaced in pinning. Scutellum with broad, flat, black scales on all three lobes. Postnotum dark brown, somewhat paler in the mid-line. *Abdomen* with tergites entirely dark. Sternites also apparently dark-scaled. Wing veins and knob of halteres dark. Legs dark without any special modifications. *Terminalia* very much as in *U. pandani*.

Adult female.

Very much as in the male.

Pupa (fig. 6).

The following description is based on three pelts associated respectively with the holotype, allotype and male paratype. The principal differences from the pupae of *U. pandani* are as follows. *Cephalothorax* with seta 3 bifid or trifid, 4 tetrafid, 5 with 4–5 branches, 6 single or bifid, 8 with 4–6 branches. *Metanotum* with seta 10 trifid to pentafid and 12 bifid to pentafid. *Abdomen* segment I with 2 single or bifid, 4 and 5 of moderate length, 7 bifid. Segment II with 1 bifid or trifid, 2 bifid, 3 and 4 single or bifid. Segment III with 1 and 2 single or bifid. Segment IV with 1 bifid or trifid, 2 bifid or trifid, spinelike, 4 bifid, 6 posterior to 7. Segment V with 2 single or bifid, spinelike, 4 single or bifid, 6 posterior to 7, 7 single or bifid. Segment VI with 2 single or bifid, spinelike, 4 single or bifid, 6 more than twice as long as 7. Segment VII with 1 single or bifid, 2 single or bifid, spinelike, 4 very long and stout, single or bifid, 6 about as long and nearly as stout as 7, lightly plumose, single or fimbriated at the tip, 7 with 3–6 branches. *Paddles* with seta 1 simple.

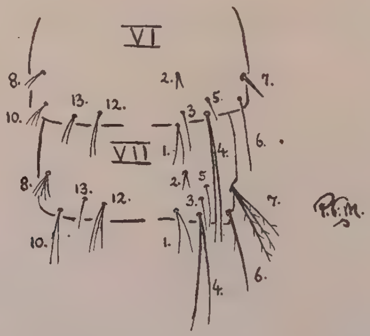


Fig. 6.—*Uranotaenia browni*, sp. n. Segments VI and VII of pupal abdomen.

Larva (fig. 7).

This cannot be attributed with certainty since we have no associated pelts. However, the whole larva described below, together with others like it, was obtained from the same fallen leaves of coco-de-mer as the associated pupae described above. The only other larva obtained from these leaves was a single, rather dark, but otherwise quite typical larva of *U. pandani*. That this larva ought to be associated with *U. browni* seems most unlikely in view of the difference between the pupa of this species and that of *U. pandani*. To make such an association would imply the presence of a fourth species of *Uranotaenia* since the pupal differences are undoubtedly of specific order. Of the existence of such a species there is at present no other indication. The general appearance of the larva attributed to *U. browni* is most remarkable. Like the larva of *Culex stellatus* (*infra*) its thorax and abdomen are covered by a dense matting of strongly developed stellate setae, very much as in most larvae of the genus *Tripteroides*. In view of the presence of a comb plate in combination with a strongly developed ventral brush and of the characteristic shape of the head setae, however, no hesitation is felt in assigning them to the genus *Uranotaenia*. The ornamentation of the siphon is unique among Ethiopian mosquitos and is approached only by some Neotropical Sabethini (see Lane & Cerqueira, 1942) and by the Oriental genus *Topomyia* (see Brug, 1931*a*). The position and appearance of the siphonal tufts is, however, precisely as in typical *Uranotaenia*. The general facies of these larvae is further discussed below in connection with *Culex stellatus*. The description which follows is based on a single fourth-instar larva with the data detailed above, except where otherwise stated. *Head* rather square in shape, about as broad as long. Antenna short, smooth. Antennal seta short, very delicate, apparently unbranched, situated at about three-fifths the distance from base to apex. Head seta A with three branches which are relatively slender but are tapered in a manner strongly reminiscent of those species in which the head setae are in the form of spines. B single, slender but even more spinelike than the branches of A. C long and slender, single. All these setae simple. Seta *d* minute, very delicate, apparently bifid with some secondary branching. Mentum triangular with 9 teeth on either side of the main central

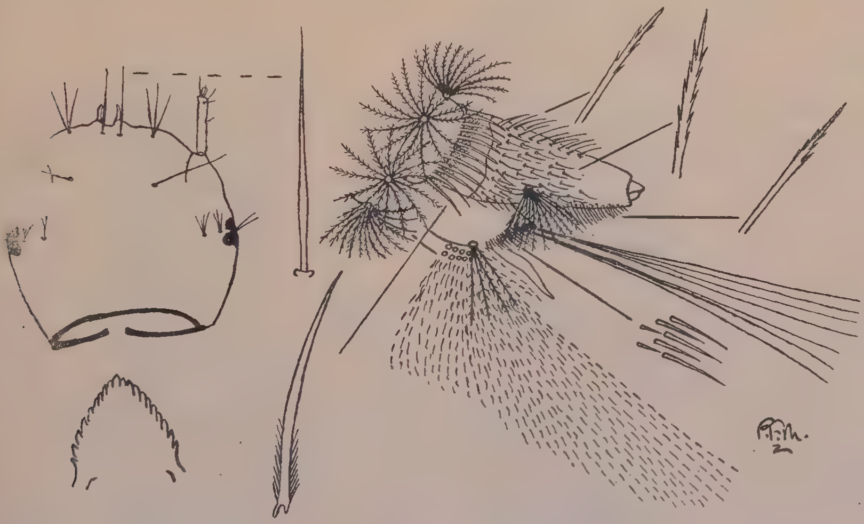


Fig. 7.—*Uranotaenia browni*, sp. n. Fourth-stage larva.

tooth. *Thorax* with numerous very strongly developed stellate setae, the lateral setae mostly long, stout and plumose. *Abdomen* with strongly developed stellate setae. Very long but slender lateral setae present on the first six segments. Comb, set on a very well-marked comb plate, composed of 11 very long, stout, curved spines with basal secondary denticles. Siphon with index just under 2 (crushed), entirely covered with long curved spines, except for an apico-dorsal area which is bare. The spines of all three groups, dorsal, lateral and ventral, are fimbriated but this is most easily seen in the lateral group which lie flatter than the others. They are not organised into a definite pecten. Siphonal tufts with about 10 plumose branches, situated at about two-fifths the distance from base to apex. Saddle apparently not quite complete, its distal edge very strongly spiculate. Saddle hair damaged, apparently tetrafid. (In an accompanying third-instar or perhaps small fourth-instar larva from the same breeding place it is somewhat longer than the saddle with four stout plumose branches.) Upper caudal seta with four branches, lower trifid. Ventral brush composed of five pairs of setae with sclerotised bases forming a well marked barred area. These setae are missing in the specimen under consideration but in the accompanying larva referred to above they are long, stout, plumose and strongly branched, the distal ones being of great length, approximately equal to the caudal setae. Anal papillae subequal, about the same length as the saddle, very sharply pointed.

Taeniorhynchus uniformis (Theo.).

The only previous record of this genus from the Seychelles is that of Theobald (1912, as " species ? (probably new)"). I have been unable to discover any of Theobald's specimens which are stated to have been preserved in spirit and to have been in very poor condition. It seems that his species may very well have been the present one. E.S.B.'s specimens are in good condition and seem quite typical. The identification was confirmed by dissection of the terminalia.

Aëdes (Ochlerotatus) vigilax ssp. **vansomerenae,** ssp. n.

Adults of this subspecies differ from type form *Aë. vigilax* Skuse (1889 and see Mackerras, 1927) and from ssp. *ludlowae* (Blanch.) (1905 and see Knight & Hull, 1951) in having a greater proportion of the scales on the posterior pronotum pale, in the presence of strongly developed lateral prolongations of the pale tergal bands on the abdomen of the male and in not having the terminal appendage of the male claspette hooked. The larva differs in usually having more branches in the antennal tuft, in having more teeth in the mentum and, apparently, in having the comb spines more delicately fringed with less tendency to thickening of the median denticle. The males also differ from the description of ssp. *ludlowae* given by Knight & Hull in having the lateral patches of broad pale scales on the vertex narrowly interrupted by dark scales. A similar condition is, however, shown by a male of ssp. *ludlowae*, from Manila, in the British Museum. The present form differs from Knight & Hull's description of the Philippines subspecies in usually having 6 instead of 3–4 bristles on each lobe of the male ninth tergite. It is, however, presumed that the figure given by Knight & Hull refers only to bristles on the distal edge of the lobe and does not include the two supernumary bristles occurring on the body of the lobe both in the Seychelles specimens and in the specimen from Manila. Finally it seems probable that the antenna of the larva has fewer spicules than in either the type form or ssp. *ludlowae*. Published descriptions of the larva of the type form (Cooling, 1924*b*; Woodhill & Pasfield, 1941; Lee, 1944) are, however, incomplete. A larva from Madoera I., N.E. of Java, in the British Museum, is probably the one described by Brug (1924). It has very much more slender clypeal spines than the Seychelles larvae in addition to having the antennae much more strongly spiculate. It may perhaps belong to the type form since in both respects it differs from Knight & Hull's description. It seems clear that *Aëdcs vigilax* is closely related to *Aëdcs frycri* (Theo.) (1912) which was originally found in the Aldabra Group and is believed to occur also in Madagascar and on the coasts of Kenya and Mozambique and to *Aë. dufouri* Hamon (1953*a*) which is at present known for certain only from Réunion. The present species differs from *Aë. dufouri* in the shape of the male style. Unfortunately no topotypical males of *Aë. frycri* are available for comparison but only males from Kenya. The larva of *Aë. vigilax vansomcrcnac* is not known for certain but, since it is the only *Ochlcrotatus* occurring in the Seychelles and since larvae which clearly belong to the *vigilax* group were obtained from two out of the three pools from which the adults were bred, the attribution seems virtually certain. The same argument applies to *Aë. frycri* which, if the attribution of larvae is accepted, can be distinguished from the present species by the shape and number of comb spines. The description of the adult of *Aë. vigilax vansomcrcnac* which follows is based on a holotype ♂ and allotype ♀ from Anse Lascar, Silhouette I. (coll. *E. S. Brown*, 14.ii.1953), 3 ♂ and 4 ♀ paratypes with the same data as the holotype and 2 ♂ and 1 ♀ paratypes from Dennis I. (coll. *E. S. Brown*, 1.x.1952). Two female adults from another breeding place on Silhouette I. are not included in the description because they have no associated males or early stages. They are described below under variation.

Adult male.

Head.—Palps about four-fifths the length of the proboscis. (According to Hamon they are about the same length in *dufouri* but in the Mombasa species

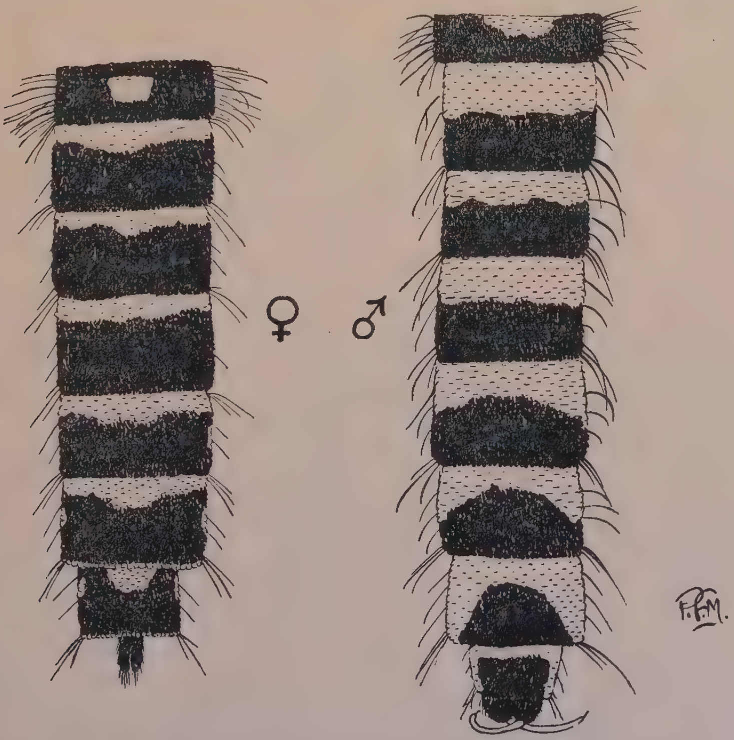


Fig. 8.—*Aëdes vigilax* ssp. *vansomerenae*, ssp. n. Abdomen in dorsal view.

the proboscis appears markedly shorter and they are about 9/10ths its length or even 19/20ths.) White spots present on upper surface at bases of ultimate and penultimate segments and half-way along the shaft. (A pale spot is also present in the latter position in the Mombasa species although Edwards (1941) does not mention it. The markings of the palps in *dufouri* have not been described.) Proboscis in most cases entirely dark above with a small number of pale scales below tending to form a spot at about half way. In one specimen, however, this spot is strongly marked and extends up the sides and, narrowly, on the upper surface. Upright scales of vertex narrow, pale yellowish in the middle, a few dark ones at the sides. Decumbent scales narrow, curved, white. Scales at sides of head broad, flat, white except for a well-marked sublateral dark stripe. *Thorax*.—Scutum covered with rather small scales which are mostly golden, mixed with some darker brown ones. A few whitish scales are present in the neighbourhood of the prescutellar bare space and on the shoulders and round the sides of the scutum and a pair of pale spots are faintly indicated on either side of the mid-line at about half way. Scutellum with narrow whitish and pale golden scales on all lobes. Prosternum bare. Propleura with broad pale scales. Anterior pronotum with pale scales, the majority narrow and curved, a few broader and flatter. Posterior pronotum with a conspicuous patch of broad white or whitish scales posteriorly and ventrally, rather smaller flat blackish scales forming a patch in the middle and narrow golden scales along the upper margin. Pleurae largely defaced in mounting. *Abdomen*.—Tergite I with a small median basal white spot. Other tergites with broad white basal bands which become progressively more deeply emarginate on the posterior segments (a strongly marked example of sexual dimorphism, see fig. 8). The markings of the abdominal tergites seem to be particularly subject to sexual dimorphism in some African *Aëdes*, notably in certain *Stegomyia* and especially

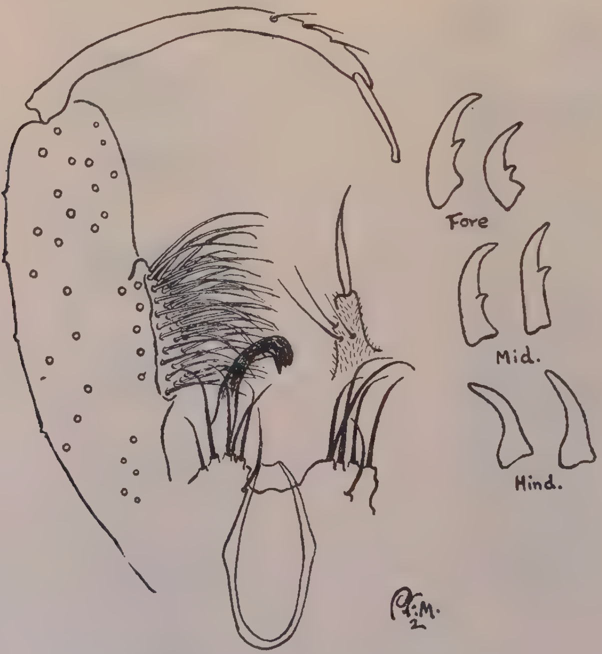


Fig. 9.—*Aëdes vigilax* ssp. *vansomerenae*, ssp. n. Male terminalia in tergal view, and female claws.

Aë. dendrophilus Edw. which also differs in mesonotal markings in the two sexes (Mattingly, 1952, 1953*a*).

Sternites mainly white scaled with dark apical bands which tend to become progressively broader on the posterior segments. *Wings.*—Length about 3 mm. Rubbed in all cases but fairly numerous pale scales apparently present at least on costa, sub-costa, first vein, fork of second, stem of fifth and sixth. Halteres rubbed. *Legs.*—All femora and tibiae heavily speckled with pale scales and with narrow but fairly conspicuous knee-spots. First three tarsal segments of fore- and mid-legs and all five hind tarsal segments narrowly banded at base. Fore- and mid-tarsi each with one small and one large claw. Both claws toothed. Hind tarsi with two small claws, untoothed. *Terminalia* (fig. 9).—Style long and slender with well developed terminal appendage which is also long and slender. Basal lobe of coxite strongly developed and densely setose, much as in many *Stegomyia* but without modified bristles. Paraprocts strongly developed, their tips hooked and toothed. Phallosome scoop-shaped, very lightly sclerotised and undecorated. Lobes of ninth tergite prominent, each with 4–6 strong bristles. Harpago much reduced, its terminal appendage narrow and spinelike.

Adult female.

As male except in the following respects. Palps about one-sixth the length of the proboscis with white scales at the extreme tip only. Proboscis mainly dark but with a few scattered pale scales on the lower surface, on the basal half only, forming a small spot at about half way. Upright scales of head dark brown. Dark interruption to lateral patch of flat pale scales broader. Scutum and posterior pronotum rubbed but perhaps with rather more dark scales than in the male. Post-spiracular area, paratergite, sternopleura and mesepimeron with large patches of broad white scales, those on the sternopleura occupying the whole of the narrow portion and the whole posterior border of the broader lower portion. Anterior border of the lower portion bare. Abdominal tergites as figured (fig. 8). Detached lateral white patches present but visible on the upper surface only on segments V–VII. Narrow pale apical bands present on VI and VII. Sternites with dark apical bands of more or less uniform depth except for segment VII which has two apicolateral dark patches. Wings with pale scales present on all veins except, perhaps, the fork of vein 4. Halteres with knobs entirely pale scaled. Mid-legs, in some cases, with a small pale spot at the base of the fourth tarsal segment. Claws as figure (fig. 7).

Pupa (fig. 10).

The following description is based on two pelts belonging respectively to the holotype and allotype. *Trumpets* short, very broad at the apex, tapering sharply to the base. Meatus about three-fifths of the greatest length. *Cephalothorax.*—Seta 1 short with 2–3 branches, 2 of moderate length, bifid or trifid, 3 of moderate length, apparently trifid, 4 moderately long, bifid or trifid, 5 somewhat shorter with 3–5 branches, 6 minute, single or bifid, 7 of moderate length with about 4–6 branches, 8 of moderate length with about 5 branches, 9 long, bifid or trifid. *Metanotum* with 10 short, very delicate with 5–6 branches, 11 stouter, single or with 2–4 branches, 12 short with about 3–5 very delicate branches. *Abdomen.*—Segment 1 with seta 1 well developed with about 15 main branches which are further subdivided into very delicate secondary and tertiary branches, 2 minute, single, 3, 4, 5 and 6 all very short with about 4–5, 3–5, 4–6 and 4–5 branches, respectively, 7 minute, single to trifid, 10 very short with about 6 branches. Segment II with seta 0 minute, single, 1 minute with about 8 branches, 2 minute, single, 3 rather stout and dark, very short with about 5 branches, 4, 5 and 6 all very short and about 5–6, 4–5 and 3–6 branches, respectively, 7 minute, single, 10 very short with 2–4 branches. Segment III with

0 minute, single, 1 very short with 4–5 branches, 2 minute, single, 3 of moderate length, stout, dark, single or bifid, 4 short with 4–5 branches, 5 very short with 5–6 branches, setal ring just outside and posterior to 5, 6 of moderate length with 3–4 branches. 7 minute, single, 8 and 10 minute with about 4–8 and 4–6 branches, respectively, 12 short, trifid, 13 minute, single. Segment IV with seta 0 minute, single, 1 short with 3–5 branches, 2 minute, single, 3 very short with about 5–6 branches, 4 very long, stout, lightly plumose, single or bifid, 5 very short with about 2–3 branches, setal ring posterior to and in line with or slightly outside 5, 6 short with about 4 branches. 7 minute, single, 8 very short with about 2–4 branches, 10 very short with about 4–5 branches, 12 of moderate length with about 2–3 branches, 13 minute, single. Segment V with seta 0 minute, single, 1 of moderate length with 3–5 branches, 2 minute, single, 3 long, very slender, bifid, 4 very long, stout, lightly plumose, bifid on the only

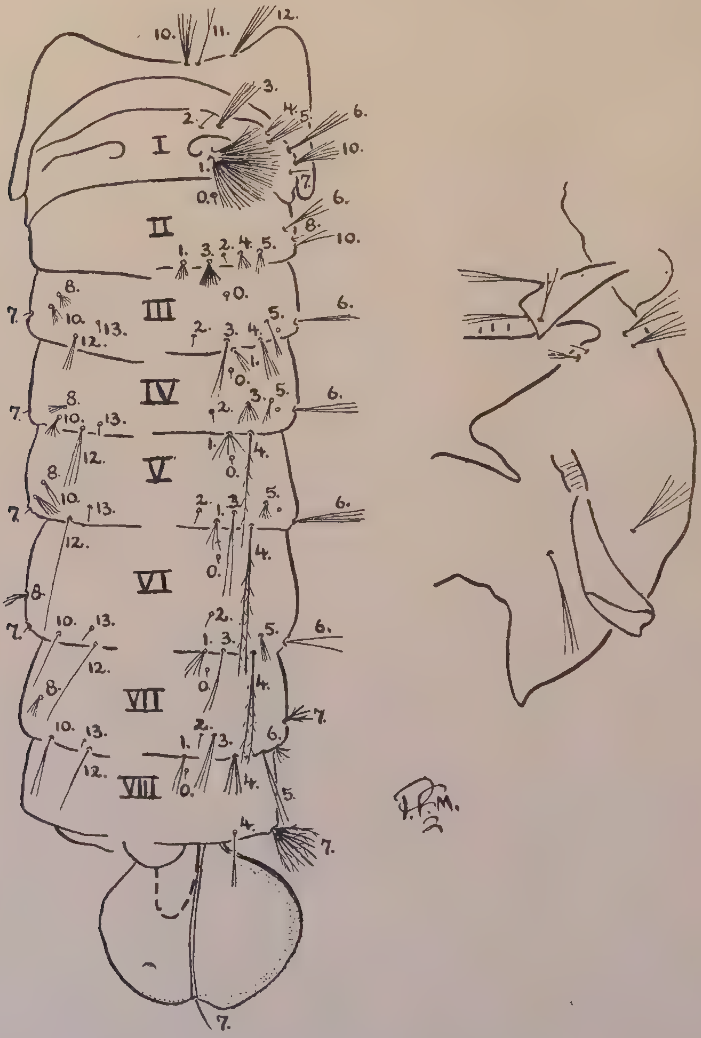

10.
11.
12.
3.
2.
4.
5.
6.
I
1.
10.
7.
0.
6.
II
8.
1.
3.
2.
4.
5.
10.
8.
0.
III
7.
10.
13.
12.
5.
6.
2.
3.
4.
1.
0.
IV
8.
7.
10.
13.
3.
5.
6.
2.
1.
4.
12.
V
8.
0.
10.
7.
13.
2.
1.
3.
5.
6.
12.
4.
VI
0.
8.
7.
10.
13.
2.
1.
3.
5.
6.
12.
8.
0.
VII
4.
7.
10.
13.
2.
1.
3.
6.
12.
VIII
0.
4.
5.
4.
7.
7.
P.F.M.
2

Fig. 10.—*Aëdes vigilax* ssp. *vansomerenae*, ssp. n. Pupa: dorsal abdominal setae on the right, ventral on the left.

pelt on which it is preserved, 5 short with about 5 branches, 6 short with about 3–4 branches, 7 minute, single, 8 very short, bifid, 10 very short with about 4–6 branches, 12 long, very slender, single, 13 minute, single. Segment VI with 0 minute, single, 1 short, with 2–4 branches, 2 minute, single, 3 short, bifid or trifid, 4 long, lightly plumose, bifid on both pelts, 5 short with 4–5 branches, 6 short, bifid, 7 minute, single, 8 very short with about 3 branches, 10 short, single or bifid, 12 of moderate length, single or bifid, 13 minute, single. Segment VII with 0 minute, single, 1 short with 2–3 branches, 2 minute, single, 3 short with 3–4 branches, 4 short with about 4–5 branches, 5 of moderate length and stoutness, bifid or rather shorter and more slender, trifid, 6 very short with about 4–5 branches, 7 short with 2–4 moderately stout branches and some secondary feathering, 8 very short with about 5–6 branches, 10 longer, single or bifid, 12 of moderate length, single or bifid, 13 minute, single. Segment VIII with 0 minute, single, 4 short, bifid, 7 short with 7–8 moderately stout, plumose branches. *Paddle* broad, rounded, the outer edge thickened on the basal half and with several rows of very minute spicules which are continued for an indefinite distance beyond seta 7. The latter short, single.

Larva (fig. 11).

The following description is based on 6 whole larvae from the batch from which the holotype and allotype were bred.

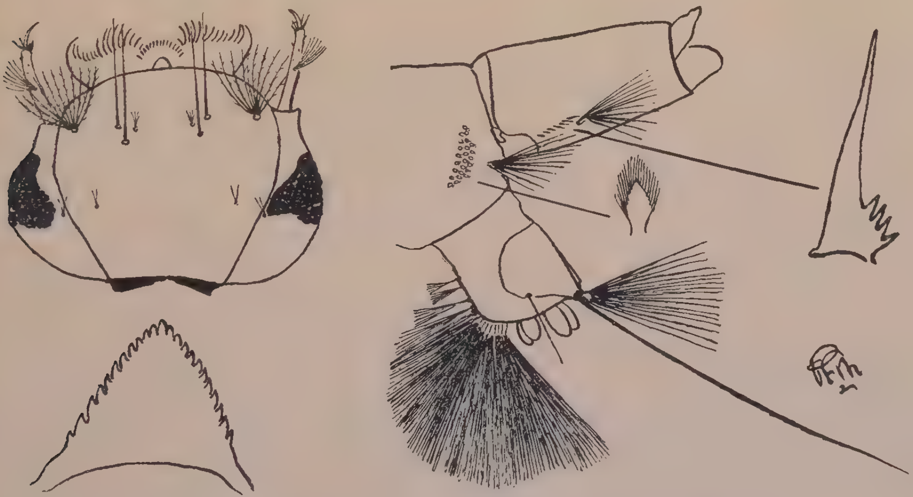


Fig. 11.—*Aëdes vigilax* ssp. *vansomerenae*, ssp. n. Fourth-stage larva.

Antenna short, less than half the length of the head, smooth except for a very small number of inconspicuous spicules on the distal half. Proximal half in most cases smooth. Tuft of 4–7 long, fairly stout branches at about half way. Mouth brushes with serrated teeth of inner bristles very strongly developed. Outer bristles short and rather stout. Seta A with about 8–10 lightly plumose branches, B and C single, apparently simple, *d* minute with about 4 very delicate branches. Mentum smoothly rounded with 11 rather narrow teeth on either side of the main central tooth. Comb of 16–32 small scales, the body of the scale frequently drawn into a point apically but the median denticle not noticeably stouter than the remainder. Siphon short, index about 1·2–1·8 in crushed specimens. Pecten of 7–10 sharply attenuated spines, each with 2–4 well marked ventral denticles. Distal spines occasionally with a dorsal denticle in addition. Siphonal tuft of 10–15 long plumose branches situated at about two-fifths of the distance from base to apex. Saddle very poorly sclerotised and incomplete. Saddle hair unbranched, short, slender, often very hard to detect. Anal papillae shorter than the saddle, the upper pair slightly longer than the lower. Upper caudal seta with about 12 branches, lower single. Ventral brush with 12–14 many-branched tufts in the barred area and 2–4 precratal tufts. A single whole larva from the same breeding place as the Dennis I. paratypes has the two most distal pecten spines each with 2 dorsal denticles.

Variation.

Two female adults from Pointe Trevor, Silhouette I. (coll. *E. S. Brown*, 12.iv.1952) and two whole larvae from Bird I. (coll. *E. S. Brown*, 1.x.1952) differ from the above description as follows:—*Adult.*—One specimen with proboscis as described above, the other with extensive pale scaling on about the basal three-fifths of the upper surface and a corresponding increase in pale scaling on the lower surface. Lateral pale patches on the abdominal tergites fused with the basal pale bands of which they form continuous lateral prolongations, though still much less extensive on the dorsal surface than in the males described above. 7th abdominal sternite with a continuous apical dark band. *Larva.*—Pecten with 10–13 spines.

Aëdes aegypti (L.).

No specimens of this species were collected. It appears previously to have been confined to the neighbourhood of Port Victoria and may have been eradicated since Harper's visit. Specimens in the British Museum contain a high proportion of pale forms (" var. *queenslandensis* " (Theo.)). The distribution and taxonomy of these forms is discussed by Mattingly (1953*a*, Appendix III and pp. 46–48). Recent work in East Africa seems to indicate that their bionomics may differ significantly from those of the dark form. It seems highly desirable that their genetics should be studied in more detail.

Aëdes albopictus (Skuse).

A few notes on the morphological characteristics of the Seychelles form are given by Mattingly (1953*a*).

Aëdes albocephalus (Theo.).

This is the species described by Theobald (1912) as *Reedomyia seychellensis* and provisionally synonymised by Edwards (1932) with *Aëdes rhecter* Dyar and later (1941) with *Aë. albocephalus*. No topotypical females from Gambia are available for comparison, but the British Museum has a female from Accra and comparison has been made with this. The agreement is very close and Edwards' provisional synonymy is therefore accepted. That the Seychelles species is the same as that occurring on the mainland or the one found on Aldabra must remain conjectural until males and early stages of the island forms are obtained. It is possible that these forms are part of a species complex similar to that found in *Ochlerotatus* (see above).

Aëdes pembaensis Theo.

The numerous specimens collected appear quite typical. This is the only known Ethiopian species of the subgenus. Doucet (1950) described a larva from Madagascar which he placed in *Skusea* under the name *Aë.* (*Sk.*) *cachani*. It seems, however, that this should have been placed in *Uranotaenia*. Monsieur Hamon tells me that he examined Doucet's type in the Paris Museum and found that it had a recognisable though rather lightly sclerotised comb plate. I have been able to confirm this from a paratype kindly sent me from the Paris Museum by Monsieur Séguy.

Culex stellatus van Someren.

The adult and early stages have been described in detail by van Someren (1947) and the larva is well figured in Hopkins (1952). The most remarkable feature of this larva is the dense matting of stellate setae covering the thorax and abdomen. These setae are closely similar to those found in the larva attributed to *Uranotaenia browni* (see above) and the two species also have very similar comb spines. The great development of stellate setae is characteristic in varying degrees of all larvae of the genus *Tripteroides* (see Baisas & Ubaldo-Pagayon, 1952) and some of these also have comb spines of the same type, *e.g.*, *Tripteroides nepenthis* (Edw.) (1926), a species breeding in *Nepenthes* pitchers. The same combination of stellate setae and very long comb spines is also exhibited by *Aëdes* (*Stegomyia*) *arboricolus* Knight & Rozeboom (1946) which is at present known only from a tree hole. Other larvae of *Tripteroides* belonging to species breeding in bamboos, pitchers, tree holes, leaf axils and other organic habitats show the stellate setae in combination with comb spines of a different kind as do the Australasian *Aëdes* (*Stegomyia*) *horrescens* Edw. (1935), the Neotropical subgenus *Howardina* of *Aëdes*, which breeds in leaf bases, flower bracts and tree holes, certain species of the Oriental and Australasian plant-axil breeding *Aëdes* (*Finlaya*) *kochi* (Dön.) group and the Palaearctic *Aëdes* (*Finlaya*) *echinus* Edw. which breeds in tree holes. In the latter, however, the setae are of rather a different type (see Edwards, 1921). Occurring as they do in so many genera and subgenera it is difficult to believe that the presence of these setae indicates any close phylogenetic affinity between the species which possess them. On the other hand they are not associated exclusively with any particular type of breeding place, except organic containers in a broad sense. The same is true of the very long lateral setae noted above in the larva of *Uranotaenia nepenthes*. Here there seems to be a partial correlation with breeding in plant pitchers within the genus *Uranotaenia*. Comparable setae are, however, to be found in other genera, in species breeding in other organic habitats. Here the most interesting comparison is perhaps with the *Eretmapodites chrysogaster* Graham group since this again shows a link with *Tripteroides* partly through resemblances between the larvae of the two genera and even more so in the astonishing fidelity with which the highly characteristic general facies of the adult *Eretmapodites* is reproduced in *Tripteroides coeruleocephala* (Leic.), one of the most remarkable parallelisms to be found among the mosquitos. (*Cf.* also *Paräedes argyrurus* Edw. (in Barraud. 1934), the status of which it is proposed to discuss in detail elsewhere.)

Culex simpsoni Theo.

None of the adults collected exhibit the pale stripe on the mid femur noted by Edwards (1941) in specimens from Mauritius and Rodriguez. The larva is somewhat variable but the degree of variability has been exaggerated. Thus the statement by Hopkins (1952) that larvae from Zululand have pecten spines "which are either simple or with one or two minute basal denticles" is apparently due to misobservation, since in fact the pecten spines of these larvae are similar to those of the Kenya larvae, one of which he figures, and have about 6–8 of such denticles. The same is true of all the larvae in the extensive range now available at the British Museum, and Hopkins' key should be amended (see Appendix II). Other variation affects the length and degree of branching of the subventral tufts of the siphon and the relative lengths of head setae B and C. The material at present available does not seem to warrant any taxonomic treatment of this variation, but larvae provisionally assigned to *C.*

simpsoni have recently reached the British Museum for the first time from West Africa (Senegal and Bauchi Plateau) and these will be described and the variation discussed in a later paper. The form of *C. simpsoni* occurring in Mauritius and the Aldabra Group differs from the mainland forms in having rather more comb spines (30–35 in Aldabra specimens in the British Museum, and the same in Mauritius specimens according to MacGregor 1927), as compared to about 20–25 in specimens in the British Museum from N. Rhodesia, Kenya, Tanganyika and S. Africa. The present collection contains fourth-instar larvae from Silhouette, Praslin, Anonyme, Bird, Cousin, Aride, Mahé, Félicité and Thérèse Islands. The number of comb spines varies in this material from 27–49 but in almost all cases it lies between 30 and 35, a good reason against regarding this species as an importation from the mainland. The siphonal tufts in all cases are approximately equal in length to the breadth of the siphon at the point of attachment. Head seta C is markedly shorter than B and single or bifid, both conditions being occasionally shown by the same larva. The pecten teeth have about 4–8 basal denticles.

Culex pipiens ssp. **fatigans** Wied.

Recent work in the United States appears to indicate that this form can and does interbreed in nature with *C. pipiens pipiens* L. (Mattingly & others, 1951). It is therefore treated here as a subspecies. More recently Dobrotworsky & Drummond (1953) have expressed the opinion that the evidence of naturally occurring hybridisation is insufficient while admitting that hybridisation takes place freely in the laboratory. The matter is under investigation by A. R. Barr at the University of Minnesota. Available data regarding the position in Africa are very few. A small number of possible intermediates from South Africa may or may not indicate the occurrence of natural hybridisation there. Another possible locus seems to be the boundary between the Palaearctic and Ethiopian and the Palaearctic and Oriental regions. There is at present no indication of the occurrence of hybridisation at intermediate altitudes on mountains but much more material from such altitudes needs to be examined and the seasonal factor should be taken into account. Biological differences appear to indicate the presence of distinct strains of *fatigans* in West and in East Africa and this in turn suggests the entry, whether active or passive, of more than one diverse element into Africa from different sources. A detailed study of variation in the DV/D ratio in the Seychelles form would be of interest and the possibility of laboratory hybridisation with *Culex scotti* should certainly be investigated.

Culex scotti Theo.

This is a very interesting species apparently annectent between *Culex pipiens* on the one hand and *Culex musarum* Edw. and *Culex hancocki* Edw. on the other, having male terminalia like those of the former and external characters resembling those of the latter. Knight (in Mattingly & others, 1951) has stressed the resemblance to *C. pipiens* while Hopkins (1952) has emphasised the resemblance to *C. musarum* and *C. hancocki* and, by reason of this resemblance, has suggested that *C. scotti* is probably a plant-axil breeder. Edwards (1941) treated it as an annectent species. None of these authors has noted the fact that its very striking mesonotal markings are almost identical with those of *Culex simpsoni*, an important point to bear in mind since it would seem that the two species occur together in the neighbourhood of Grande Anse, Praslin. The affinities of *C. scotti* are further discussed below under Zoogeography.

DISTRIBUTION.

The following records are from material collected by E. S. Brown, except where otherwise stated.

Uranotaenia pandani.

Mahé I., forest behind Cascade, about 1,500′, ii.1909; Anse aux Pins, i.1907; Mare aux Cochons (Theobald, 1912); Port Victoria area; viii.1945 (Harper, 1947, date from specimens in B.M.); Val Mer, 9.vi.1952; Canelles, 7.viii.1952, 16.viii.1952, 16.ix.1952, 30.xii.1952. Anonyme I., i.1907 (Theobald, 1912), 31.vii.1952. Praslin I., L'Amitié, 17.vi.1952, 21.viii.1952; Vallée de Mai, 22.vi.1952; Baie Ste. Anne, 25.viii.1952. Cerf I., 14.viii.1952. Grande Soeur I., 25.i.1953. Félicité I., 25.i.1953. Round I. (Praslin), 31.i.1953.

It now appears that this species occurs in Madagascar where it has been recorded under the name *U. pauliani* (Doucet, 1949*b*), see above.

Uranotaenia nepenthes.

Silhouette I., in "highest damp forests (over 2,000′)" 29.vii.1908 (Theobald, 1912); Morne Pot-à-Eau, 16.iv.1952; Congoment, 20.iv.1952. Mahé I., 1908–1909 (as *U. pandani* var., Theobald, 1912, as *U. nepenthes*, Edwards, 1941); Port Victoria area, 1945 (Harper, 1947).

This species has also been recorded from Madagascar (Edwards, 1941; Paulian, 1950; Doucet, 1950) but it is considered that these records need confirmation (see above).

Uranotaenia browni.

Praslin I., Vallée de Mai, 22.vi.1952.

This species is at present known only from the type locality.

Taeniorhynchus uniformis.

Praslin I., Grande Anse, 7.i.1953, 27.i.1953. Mahé I., Barbarons Estate, 1908 (as *T.* species ?, Theobald, 1912).

The identity of the Mahé species is uncertain (see above). *T. uniformis* is very widely distributed outside the Seychelles, occurring throughout tropical Africa, in Madagascar and eastwards through the Oriental region to the Solomons, northern Australia and Japan (see Edwards, 1941; Farner & others, 1946; and Brug & Bonne-Wepster, 1947). A specimen of uncertain identity recorded by MacGregor (1927) from Mauritius may have belonged to this species.

Aëdes vigilax ssp. **vansomerenae.**

Silhouette I., Pointe Trevor, 12.iv.1952; Anse Lascar, 14.ii.1953. Bird I., 27.ix.1952. Dennis I., S.W. corner, 29.ix.1952.

The type form of *Aëdes vigilax* Skuse is known from Australia, Timor, New Guinea, New Caledonia and New Hebrides. A subspecies from the Philippines was described by Knight & Hull (1951). The same subspecies apparently occurs in Siam and Formosa. Other forms of unknown status occur widely in the East Indies from Sumatra to Celebes (Brug & Bonne-Wepster, 1947).

Aëdes aegypti.

Mahé I., Port Victoria (as *Stegomyia fasciata* F., Theobald, 1903 and 1911, as *Aë. aegypti*, Harper, 1947 and Mattingly, 1953*a*).

The fact that this mosquito was not taken by Mr. Brown emphasises its rarity in the Seychelles where it is apparently restricted to the neighbourhood of Port Victoria. This curious distribution has been discussed at length elsewhere (Mattingly, 1953*a*). The species is cosmotropical but has a restricted distribution in some groups of islands in the Oriental and Australian parts of its range (see Bonne-Wepster & Brug, 1932, and Farner & others, 1946. For Mauritius see Mattingly, 1953*a*).

Aëdes albopictus.

Mahé I., Capucin, 27.iv.1906 (as *Aë. scutellaris* (Wlk.), Theobald, 1910 and 1912. Date from specimens in B.M.); Cascade Estate, Morne Blanc, 1908 (as *scutellaris*, Theobald, 1912); Anse aux Pins, 1908 (as *scutellaris*, Theobald, 1912), 14.v.1952; Port Victoria, 28.iii.1906 (as *scutellaris*, Theobald, 1910 and 1912. Date from specimens in B.M.), 1945 (as *albopictus*, Harper, 1947), 6.viii.1952; Anse Royale, Bel Air, 1945 (Harper, 1947); Grand Bois, 6.xi.1952; Grande Anse, 28.iv.1952, 6.vi.1952, 8.vi.1952, 11.x.1952; Val Mer, 9.vi.1952; Anse Étoile, 25.ii.1952; Bel Ombre, 29.vi.1952; Anse la Mouche, 6.vi.1952; Anse Boileau, 2.vii.1952. Praslin I., 1908 (as *scutellaris*, Theobald, 1912); St. Sauveur, i.1953; Baie Ste. Anne, 25.vii.1952; Grande Anse, 23–31.v.1952, 25.vi.1952; Vallée de Mai, 25.v.1952, 22.viii.1952, 24.viii.1952; L'Amitiée, 21.viii.1952. Silhouette I., ix.1908 (as *scutellaris*, Theobald, 1912). Dennis I., 1908 (as *scutellaris*, Theobald, 1912). Long I., 1908 (as *scutellaris*, Theobald, 1912), 1945 (as *albopictus*, Harper, 1947). Ste. Anne I., Round I. (Mahé), 1945 (Harper, 1947). Cousin I., iii.1953. Ile Platte, iii, iv and v:1952. Anonyme I., 31.vii.1952. Cerf I., 14.viii.1952. Round I. (Praslin), 31.i.1953.

Outside the Seychelles this species is widely distributed in Madagascar, Mauritius, Réunion, the Amirante Islands, Coetivy I. and eastwards through the Oriental region to Timor, Celebes, the Philippines and Japan. Eastwards from here it is known with certainty only from the Mariana and Hawaiian Islands, apart from a temporary introduction into north-western Australia. Its total absence from the African mainland is very remarkable. For details see Bonne-Wepster & Brug (1932), Farner & others (1946), Brug & Bonne-Wepster (1947) and Mattingly (1953*a*).

Aëdes albocephalus.

Mahé I., near Morne Blanc, x–xi.1908. Silhouette I., in high forest, viii.1908 (as *Reedomyia seychellensis*, Theobald, 1912). Dennis I., viii.1908 (as *R. seychellensis*, Theobald, 1912), 1.x.1952. Bird I., 27.ix.1952.

As noted above, the identification of this species with *Aë. albocephalus* is provisional. The latter is widely distributed in the African savannas from west Africa across to Uganda and down through the Katanga into S. Rhodesia. Along the east coast it has been found from Ganda in Kenya (specimens recently sent to the British Museum by Mrs. van Someren) through Tanganyika (Edwards, 1941) and Mozambique (Rebêlo & de Carvalho Pereira, 1943) to Zululand and Natal and as far round as Mossel Bay in Cape Province (Edwards, 1941). *R. seychellensis* was also recorded by Theobald (1912) from Aldabra (see Appendix I).

Aëdes pembaensis.

Mahé I., Port Victoria, 1945 (Harper, 1947), 9.vi.1952. Praslin I., Vallée de Mai, 25.v.1952; Grande Anse, 23.v.1952, 26.v.1952, 13–23.vi.1952, 17.vi.1952, 25.vi.1952, 22.viii.1952, 23.viii.1952, –.i.1953; St. Sauveur, 30.viii.1952, 15.x.1952; Baie Ste. Anne, 25.viii.1952.

This is a coastal species known also from Madagascar and coastal regions of Kenya, Tanganyika and Mozambique. For details see Edwards (1941), Rebêlo & de Carvalho Pereira (1943) and Doucet (1950).

Culex stellatus.

Mahé I., Port Victoria area, 1945 (as *Culex* sp. nov., Harper, 1947, as *C. stellatus*, van Someren, 1947). Praslin I., Grande Anse, 29.v.1952.

This species is at present known only from the Seychelles. The zoogeography of the small group to which it belongs is discussed below.

Culex simpsoni.

Mahé I., Port Victoria area, 1945 (Harper, 1947); Grande Anse, 10.v.1952; Sans Souci, 28.xii.1952. Ste. Anne I., 1945 (Harper, 1947), 7.ii.1953. Round I. (Mahé), 1945 (Harper, 1947). Félicité I., 25.i.1953. Cousin I., 26.i.1953. Praslin I., Grande Anse, 1.ii.1953; Newcome, 15.vi.1952; L'Amitié, 30.viii.1952. Bird I., 27.ix.1952. Ile Aride, 20.x.1952. Thérèse I., 26.iv.1952. Silhouette I., near Pointe Trevor, 12.iv.1952; La Passe, 21.iv.1952, 22.iv.1952. Anonyme I., 31.vii.1952.

This species is widely distributed throughout east Africa from the Sudan to Cape Province. It has recently been recorded from S.W. Arabia (Knight, 1953) and there is reason to suppose that it occurs also in the savannas of west Africa (see above).

Culex pipiens ssp. **fatigans.**

Mahé I., Port Victoria, undated (Theobald, 1912), 1945 (Harper, 1947), 16.v.1952, 8.viii.1952; Anse la Mouche, 6.vi.1952. Ste. Anne I., 1945 (Harper, 1947). Praslin I., Grande Anse, 1.ii.1953. Ile Platte, 4.v.1952. Félicité I., 25.i.1953.

This species is cosmotropical but it is not equally abundant in all parts of its range. Thus it is much commoner in east than in west Africa (Mattingly, 1954*a*). For distribution maps see Farner & others (1946) and Mattingly & others (1951).

Culex scotti.

Mahé I., Cascade Estate, about 1,000′, x.1908, xi.1908; near Morne Blanc, 1,000′, x–xi.1908. Silhouette I., forests about 1,000′ and more, viii–ix.1908 (Theobald, 1912). Praslin I., Grande Anse, 29.v.1906, 30.v.1906, 1.vi.1906 (Edwards, 1941, details from labels attached to specimens in B.M.).

This species is known only from the Seychelles.

ZOOGEOGRAPHY.

The insect fauna of the Seychelles was thoroughly analysed by Scott (1933), who gives a figure of 70 per cent. endemicity for the Diptera and 65 per cent. endemicity for the insects as a whole. Compared with this the figure of 16 to 31 per cent. endemicity given here for the mosquitos (the endemicity of the Seychelles *Aëdimorphus* and of *Uranotaenia nepenthes* being considered doubtful) may seem very low and might be taken to support the view, widely held, that the mosquitos are a group especially prone to human introduction. As against this there are good reasons for believing Scott's figures to be too high. Thus in his paper (p. 369, footnote) five out of eight species of mosquitos are regarded as probably endemic. By current criteria, however, only one or at most two of these species would be so regarded. In the opinion of the present author the endemicity rate of any group in the Seychelles is likely to depend to a large extent on how thoroughly that group has been collected in Madagascar.

Genus **Uranotaenia.**

Edwards (1932) divided this genus into two groups (*Uranotaenia s. str.* and *Pseudoficalbia*), placing *U. nepenthes* and *U. pandani* in *Pseudoficalbia*. Later (1941) he subdivided these groups into sub-groups A, B, C and D, but with reference to the Ethiopian region only. Belkin (1953*a*) has separated *U. quadrimaculata* Edw. and related Papuan species into a distinct sub-group. Despite the striking differences between their larvae it is my opinion that the three Seychelles species of *Pseudoficalbia* are very closely related. I do not believe that the larval characters afford a true index of affinities. (For a comparable case see De Beer (1951) on *Culex mouchcti* Evans.) Close relatives of the Seychelles species occur in Madagascar and, as far as can be judged, in the Malayan sub-region. (The names of this and other Oriental sub-regions are here employed in the sense attributed to them by Christophers (1933).) Two seemingly slightly less closely related groups, the *U. ornata* Theo. and *U. fusca* Theo. groups, occur on the African mainland. On the basis of material at present available it would seem that the closest relative of the Seychelles group of species to be found elsewhere in the world is *U. moultoni* Edw. (1914*b*) from Borneo. The early stages of this species are unknown, but both sexes of adult are available and they are extremely similar to *U. nepenthes*. *U. tubanguii* Baisas (1935) may also be closely related but I have seen no material of this species. *U. quinquemaculata* Bonne-Wepster (1934) is another possible member of the group but it is at present known only from a unique female adult. A number of species recently described from Madagascar seem to be possible members of the group (*U. combesi*, *U. lavieri* and *U. tsaratananae*, Doucet, 1950; *U. grenieri* and *U. brumpti*, Doucet, 1951*b*), but these species are at present known only as larvae. The *U. ornata* and *U. fusca* groups are clearly related but perhaps more remotely, since it seems that the former may have independent affinities with the Indomalayan species, resembling them in having large areas of pale yellow scales on the mesonotum (*U. brevirostris* Edw., 1915 and 1926: *U. lutescens* Leic., 1908). On the evidence it seems best to regard the Seychelles species as a Malagasy group with Malayan affinities. It seems possible that they have differentiated in the Seychelles from a common stock and that the larval differences are secondary. Certainly the wide ecological differences afforded by the coconut plantations favoured by *U. pandani*, the high forests of Silhouette and Mahé and the strange vegetation of the Vallée de Mai would seem to afford ample scope for this type of speciation. (For a detailed study of a comparable type of "ecological" speciation see Pittendrigh, 1950*a* and 1950*b*, on the *Anopheles* of the Trinidad Bromelias.)

Genus **Aëdes** subgenus **Ochlerotatus.**

Scott (1933) has stressed the "overwhelmingly strong Oriental or Indo-Australian" element in the Seychelles insect fauna of which both *Uranotaenia* and the present group may be taken as representative. The Seychelles subspecies of *Aë. vigilax* appears to be most closely related to ssp. *ludlowae* (Blanch.) 1905 (for which see Knight & Hull, 1951) which has been recorded from the Philippines and which would seem, from material in the British Museum, to occur also in Formosa and Siam. The type form is Australian and a third form, probably distinct, occurs in the East Indies (Brug & Bonne-Wepster, 1947) but of this the British Museum has only a larva. Edwards (1932) placed *Aëdes vigilax* and the closely related *Aëdes fryeri* (Theo.) (1912) from Aldabra and Cosmoledo Islands in a group of *Ochlerotatus* (Group A) of which all the other members were either New World or Australian. To this group may be added *Aëdes dufouri* Hamon (1953*a*), recently described from Réunion. The species of the same group occurring in the Mombasa area (Edwards, 1941), on the Mozambique coast (Rebêlo & de Carvalho Pereira, 1943), and in Madagascar (Edwards, 1941) agrees with *fryeri* rather than *dufouri*, but its identity cannot be finally established until further material is available. Some revision of Edwards' group A has recently taken place (Marks, 1949) but the general features of its distribution remain unaffected. The zoogeography of the Australian members of the group was discussed by Mackerras (1927, 1950) who recognised their New World affinities but drew the conclusion that they probably represented a Lemurian or Gondwanaland element in the Australian fauna rather than an "antarctic" one. He considered this group to have been Neotropical in origin and to have entered Australia from the north by way of Gondwanaland or its equivalent in a chain of islands. Certain Australian *Ochlerotatus*, belonging to other groups, also have New World affinities and these he regarded as holarctic in origin and as having migrated southwards down the western side of the Americas and entered Australia from the south by way of an Antarctic route. Some support to this latter interpretation is afforded by the recent discovery in South Africa of two species of *Ochlerotatus* very closely related to Australian members of the "Antarctic" group (Muspratt, 1953; Mattingly, 1954*a*). Marks (1949) distinguished three sub-groups among the Australian members of group A. In one of these she placed *Aëdes vigilax* and *Aëdes rubrithorax* (Macq.). To these I would add *Aëdes fryeri* and *dufouri* and *Aëdes edgari* Stone & Rosen (1952) from Tahiti to form the *Aëdes vigilax* group *sensu stricto*. If Mackerras' views are correct the members of this group occurring in the Seychelles might represent a Gondwanaland relict. Alternatively it seems possible that *Aëdes vigilax* is, as Mackerras suggests, an Australian invader of the Oriental region and that it reached the Seychelles from the east after this invasion took place. The possibility that it is a recent human introduction seems to be contraindicated by the association between the Seychelles and the Borneo-Philippines area already demonstrated for *Uranotaenia* and by the evidence of speciation in the Aldabra and Mascarene groups of islands. As to its method of introduction it is perhaps worth noting that Cooling (1924*b*) emphasises its liability to migrate for long distances with the wind. The general question of the relation of the Seychelles fauna to that of Australia has been discussed by Harrison (1928).

Genus **Taeniorhynchus.**

As regards the almost equally wide distribution of *T. uniformis* in the Ethiopian and Oriental regions little can be said. Adults of this and related species tend to enter houses shortly before and leave very shortly after feeding and the early stages develop attached to the subaqueous parts of water plants, notably *Pistia*. On both these counts this seems an unlikely species to have been distributed by man. Large masses of *Pistia* are frequently swept out to sea by flooded rivers and it would be interesting to know how long the larvae can survive in sea water. The present distribution of this species and its allies could be adduced in support of almost any theory regarding the origins and affinities of the Seychelles fauna. A significant fact in this connection is perhaps the occurrence of a very closely related species, *T. africanus* (Theo.) (for which see Edwards, 1941), over a large part of the Ethiopian region, but nowhere outside it. The two species appear to resemble one another very closely in behaviour and distribution and it is hard to believe that they are products of "ecological speciation". A more probable explanation is perhaps that they originally developed in isolation, *uniformis* in the Oriental and *africanus* in the Ethiopian region and that the presence of *uniformis* in the latter region is the result of a comparatively recent invasion.

Genus **Aëdes** subgenus **Stegomyia.**

The zoogeography of the Ethiopian species of this subgenus has been discussed in detail elsewhere (Mattingly, 1952 and 1953*a*). *Aëdes aegypti* is found throughout the tropics and sub-tropics of the world. It appears to have been widely distributed by man but has a restricted distribution on a number of islands in various parts of its range (Farner & others, 1946; Bonne-Wepster & Brug, 1932; MacGregor, 1927), a fact which is in accordance with its apparently very limited distribution in the Seychelles. It appears to belong to the Ethiopian group of *Stegomyia* but is not a typical member of this group and its origins are obscure. Its only known close relatives are two remarkable pale species apparently confined to Mauritius. A pale form of *Aë. aegypti* is found in the Red Sea area and in northern Australia and this appears to form a large element in the Seychelles *aegypti* fauna just as it does in Mauritius (Mattingly, 1953*a*). It seems quite clear that, in the case of the Seychelles, *Aë. aegypti* is a recent human introduction.

Aëdes albopictus is found very abundantly in the Mascarenes and in Madagascar. It is mainly Oriental in distribution but has been found as far north as Pekin and has a very restricted distribution in the Australian region, most, if not all, of which has probably resulted from human introduction. It clearly represents an Oriental element in the Seychelles fauna. The fact that it has not been found anywhere on the African mainland, even in the Mombasa area, militates against the theory that it has been introduced into the Seychelles by man and its much greater abundance vis-à-vis *Aë. aegypti* tends to confirm this.

Genus **Aëdes** subgenus **Aëdimorphus.**

The affinities of the Seychelles representative of this subgenus cannot be ascertained with certainty until the male and early stages are known. The very close resemblance of the female adults to those of *Aë. albocephalus*, however, would seem to render it almost certain that it belongs to this group. Specimens of *Aë. albocephalus* from the east coast of Africa differ from those from other parts of the range in frequently having all or most of the scutellar scales narrow. It would thus seem that two geographical forms are involved but it is a remarkable fact that both the original series of *Reedomyia seychellensis* and Mr. Brown's specimens have all or most of these scales broad and so conform rather to the west and central African form than to the east and south African one. It is possible that the two forms are climatypes since Marks (1954) has shown that the shape of such scales can be abruptly modified by changing the temperature of the larval environment. *Aë. albocephalus* differs from almost all the other Ethiopian *Aëdimorphus* in having the male style strongly forked (Edwards, 1941, fig. 54*b*). A similar structure is found in *Aë.* (*Aëdim.*) *lamborni* Edw. (*loc. cit.*, fig. 55*a*), an East African highland species and its close relative *Aë. boneti* Gil Collado from Fernando Po and the Cameroons. Elsewhere in this subgenus the cleft style is shown in a marked form only by the remarkable species *Aë. nummatus* Edw. from northern Bengal and Assam (Barraud, 1934, fig. 59*i*), a tree-hole breeding species which Knight & Hull (1953) regard as annectent to the subgenus *Stegomyia*. Edwards (1932) grouped *Aë. albocephalus* with a number of other Ethiopian species and with the N.W. Indian *Aë.* (*Aëdim.*) *culicinus* Edw., but the larval characters, the occurrence of narrow scales on the scutellum and the unusual development of the basal lobe of the male coxite all suggest an affinity with certain species in his Group F, a purely Ethiopian group. It seems that the affinities of this species are Ethiopian and perhaps more remotely Indian, but certainly not Malayan as in others already discussed. It is a remarkable fact that only two species of this large subgenus have been recorded from Madagascar, both very recently (Doucet, 1951*a*, *b*) although it is very strongly represented on the African mainland. The fact that neither of these species is closely related to *Aë. albocephalus* strengthens the impression that this species probably represents, in the last analysis, an Indo-Arabian element in the Seychelles fauna.

Genus **Aëdes** subgenus **Skusea.**

Among the five known species of this small subgenus, *Aë. pembaensis* is the only one known to occur in the Ethiopian region. (For "*Aë. cachani*" Doucet, see above, p. 84.) Among the remaining species *Aëdes amesi* (Ludl.) (for which see Hoogstraal & Chamberlain, 1946), *Aëdes fumidus* Edw. (for which see Knight & Hull, 1952), *Aëdes dasyorrhus* King & Hoogstraal (1946) and *Aëdes* *lamelliferus* Bohart & Ingram (1946) form a rather homogeneous group distributed from Malaya and Sumatra to New Guinea and the Carolines. *Aë. kabaenensis* Brug (1939), from Kabaena, was transferred to subgenus *Geoskusea* by Knight & Hull (1952). The affinities of *Aë. pembaensis* seem to be rather with *Aë. amesi* and *Aë. fumidus*, from the Malayan and Celebes sub-regions, than with the others. On the African mainland *Aë. pembaensis* is restricted to the east coast and it clearly represents a Malayan element in the Seychelles fauna.

Genus **Culex** subgenus **Neoculex.**

As noted by van Someren (1947), *Culex stellatus* belongs to a small and rather distinct group of this subgenus (Group E of Edwards, 1941 = Group C of Edwards, 1932). The other members of this group are *Culex horridus* Edw. (for which see Edwards, 1941), which occurs in the Sudanese and Guinean savannas and along the east coast of Africa as far south as Lourenço Marques, *Culex brevipalpis* (Giles) (see Barraud, 1934) which is widely distributed from India eastwards to New Ireland, *Culex hayashii* Yamada (see Edwards, 1921, and La Casse & Yamaguti, 1950) from N.E. China, Formosa, Japan and Korea. *Culex tenuipalpis* Barraud (see Barraud, 1934, and Brug, 1931*a*) from the eastern Himalayas and (?) Java and *Culex sumatranus* Brug (1931*b*) which was wrongly included in subgenus *Culex* by Brug & Bonne-Wepster (1947) and which is known from Sumatra and (?) Hong Kong. Of these species *C. hayashii* and *C. tenuipalpis* have both acrostichal and lower mesepimeral bristles and seem to form a distinct group, while the remainder seem to be rather closer to *C. horridus* than to *C. stellatus*. All that can be said regarding the latter, therefore, is that it has relatives both in the Oriental and in the Ethiopian regions. It is surprising that no member of group E should occur in Madagascar and it is possible that one of three species (*C. coursi* Doucet, 1949*a*; *C. demeilloni* Doucet, 1950, and *C. robici* Doucet, 1950) from that island, at present known only from the larva, may eventually prove to belong to this group.

Genus **Culex** s. str.

The apparent rarity of *Culex pipiens fatigans* except in the immediate neighbourhood of Port Victoria suggests that it is a human introduction and in view of its very close association with man this must be presumed to be the case. *Culex simpsoni* is widely distributed on the African mainland and occurs also in Madagascar and Mauritius. It has close affinities with *Culex sinaiticus* Kirkpatrick (see Kirkpatrick, 1925, and Edwards, 1941) from Sinai, the Sudan, the Somalilands and S.W. Arabia and *Culex mauritanicus* Callot from North Africa. It also appears to be related somewhat more remotely to the *Culex andersoni* Edw. group from the East African highlands (see Edwards, 1914*a*, 1941, and Mattingly, 1953*b*). It seems quite clear that this species represents a Mediterranean and East African highland element in the Seychelles fauna rather than a Malayan one. Owing to the fact that its early stages are unknown, the affinities of *Culex scotti* are difficult to determine. Edwards (1941) noted the resemblance of its male terminalia to those of the *Culex pipiens* group and of its markings to those of *Culex hancocki* Edw. and *Culex musarum* Edw. in the *Culex andersoni* group and *Culex ornatothoracis* Theo. in the *Culex decens* Theo. group, the former two species occurring in the East African highlands and Uganda and the third in West Africa *sensu lato*. Knight (in Mattingly & others, 1951) stressed its affinities with the *Culex pipiens* group and Hopkins (1952) has placed emphasis on its resemblance to *C. hancocki* and *C. musarum* and suggested that it probably breeds, like them, in plant axils. None of these authors has noted the very striking resemblance between its mesonotal markings and those of *Culex simpsoni*. It would seem that, despite the discrepancy in male terminalia, it should be placed with *C. simpsoni*, *C. hancocki* and *C. musarum* in the *C. andersoni* group and that its affinities are Mediterranean and East African highland.

The principal features of the zoogeography of the Seychelles mosquitos may be summarised as follows.

1. The mosquito fauna comprises two species, *Aë. aegypti* and *C. pipiens fatigans*, which have clearly been introduced by man and eleven species which are either indigenous or must be presumed to have been introduced by some other agency.
2. Of these eleven species eight are considered to be mainly Oriental in their affinities and to be representative of the very strong Oriental element in the Seychelles fauna noted by Scott (1933) and by Holdhaus (1927–28), the latter going so far as to suggest that the Seychelles should be treated as a part of the Oriental region.
3. The remaining three species are Ethiopian or have Ethiopian affinities. One of them, *C. simpsoni*, has a close relative in the Mediterranean region and another, *Aë. albocephalus*, appears to have a relative in N.W. India. The third, *C. scotti*, is most closely related to East African highland species on the one hand and to species having Mediterranean affinities on the other. It might thus be regarded as representing a Palaearctic element in the East African highlands and Seychelles fauna. (On the subject of the " Palaearctic " element in the Ethiopian fauna, however, see Uvarov, 1953.)
4. Harrison (1928) has paid special attention to the Indo-Australian element in the Seychelles fauna with reference to the Wegener theory. This element is strongly represented among the mosquitos and all eight of the " Oriental " species referred to above have Malayan affinities.
5. Of these eight species only two, *Aë. albopictus* and *T. uniformis*, occur in the Indian sub-region. Both these species also occur widely in the Malayan sub-region and might well have entered India from there. A third species, *C. stellatus*, has relatives in both the Indian and the Malayan sub-regions. The remaining five appear purely Malayan in their affinities. The mosquitos cannot therefore be said to afford very much evidence of the land bridge between the Seychelles and India postulated by most authors. Such evidence as they do afford would seem to agree better with hypotheses based on a direct connection with the Malayan sub-region, perhaps by way of a chain of oceanic islands.
6. As against this, Edwards, in his preface to Barraud (1934), has emphasised the fact that the plant-axil and plant-pitcher mosquito fauna of India has been very inadequately collected. The discovery of members of the *Uranotaenia nepenthes* group in S.W. India would radically transform the picture. At present this group is known only from its Seychelles and Madagascar representatives *U. browni*, *U. nepenthes* and *U. pandani* and their relatives in the Malayan sub-region. Some collections have, however, recently been made from pitcher plants in Ceylon without revealing any *Uranotaenia* (Carter & Wijesundara, 1948).
7. The views of Mackerras (1927 and 1950) on the Neotropical origins of the Australian *Ochlerotatus* fauna and its entry into Australia by a southern " antarctic " route and a more northerly " Gondwanaland " one receive some support from the occurrence of three members of his " Gondwanaland " group in the Seychelles, the Aldabra and Cosmoledo group and the Mascarenes, respectively, and of two species of his " antarctic " group in southern Cape Province.
8. The Seychelles species, *Aë. vigilax vansomerenae*, however, differs from the Aldabra and Réunion species more than these do between themselves. Its affinities are with the Malayan subspecies of *Aë. vigilax* rather than the Australian type form and it may have entered the Seychelles from the east by the same route as *Uranotaenia*. This group is totally unrepresented in India and it is unlikely to have been missed there by collectors.

9. The same is true of the other littoral species in the Seychelles fauna, *Aë. pembaensis*. This whole subgenus is unknown in the Indian sub-region. It seems unlikely to have been overlooked there and is well represented in the Malayan sub-region.

10. Eight of the thirteen Seychelles species are believed to occur in Madagascar. Of the remaining five, *U. browni*, *Aë. vigilax*, *Aë. albocephalus*, *C. stellatus* and *C. scotti*, the first two and the last have relatives there. It is also thought likely that a relative of *C. stellatus* may be found among Madagascan species at present known only from the early stages. The identity of the only known Madagascan *Ochlerotatus* is uncertain but it is thought likely that it will conform rather to the species from Aldabra and Réunion than to *Aë. vigilax*. This would be in accordance with the earlier separation of the Seychelles from Aldabra than of the latter from Madagascar assumed by most authors.

11. Apart from human agency, the contribution of which has been assessed above, recent casual introduction does not seem able to account for the principal features of the Seychelles mosquito fauna. Such introduction could have taken place in recent times only from Madagascar and other islands in the western Indian Ocean, the east coast of Africa or Arabia. Neither *U. browni*, *Aë. vigilax*, *C. stellatus* nor *C. scotti* could, as far as is known, have come from any of these areas and these four species between them pose all the problems of distribution outlined above.

12. In assessing the degree of endemicity of the Seychelles fauna it would seem desirable to take close account of the extent to which the groups concerned have been collected in Madagascar. The number of Culicine mosquitos known from Madagascar has been more than trebled in the last five years and this has had a marked effect in reducing the degree of endemicity calculated for the Seychelles fauna.

Bionomics and Local Distribution.

Description of the Islands.

The Seychelles are a small group of islands in the Indian Ocean, just over 600 miles north-east of Madagascar and nearly 1,000 miles east of Mombasa. The islands are of two kinds: precipitous granitic islands of continental rock-formation, and flat coral islands. In the main Seychelles group dealt with in this paper, only Dennis I. and Bird I. and Ile Platte belong to the latter category. Nearly all the islands lie between the Equator and latitude 5° south, and the climate is hot, and at certain seasons humid. The temperature varies little throughout the year, ranging between 75°F. and 85°F. The rainfall in different parts of Mahé (the main island) and in different years varies between 70 and 135 inches annually.

The granitic islands are steep and rugged, rising often to over 2,000 ft. on Mahé and Silhouette, and at one point to almost 3,000 ft. There are abundant rocky outcrops on the slopes, with fertile valleys between. Coconuts form the principal crop on all islands, and are cultivated both on the narrow coastal plains and on the lower slopes and in the hillside valleys. Towards 1,000 ft. in most places coconut plantations pass into forest which has been everywhere more or less interfered with by man, and only on the highest mountains of Mahé and Silhouette does the condition approach that of the original primary forest.

Breeding Places.

In the limited time available, during the course of other work in the islands during 1942 and early 1943, observations were made on the mosquito fauna. The main object was to obtain information about the breeding places of the different species. This quest was by no means exhaustive, but the habitats from which larvae were collected were varied, and include many found in the less inhabited parts and in a number of different islands. The information therefore extends or supplements that obtained by Harper (1947), who confined his attention principally to the thickly populated area in and around Port Victoria and on one or two of the smaller islands in the harbour.

Of the eleven species of mosquito found (two earlier records, *Aëdes aegypti* and *Culex scotti*, were not confirmed by the present author), seven were encountered in their larval habitats. Larvae or pupae were collected from 52 habitats in all, and when opportunity occurred adults were reared from them. A great many other habitats were examined which did not produce mosquitos in any stage, but these are not taken into account in this paper.

It should be noted that one type of habitat was not systematically studied, namely leaf axils. Plants existing in the Seychelles which have been recorded in other countries as harbouring mosquitos in their leaf axils include the following:—*Musa* (banana), *Colocasia*, *Pandanus* (screw-pine), *Ravenala* (scarce in the Seychelles), *Ananas* (pineapple), *Dracaena*, *Sanscvieria*, *Canna* (see Haddow, 1948). It is possible that some or all of these are breeding places of some importance, but no evidence was obtained.

TABLE I.

The number of occasions on which immature stages of each species were recorded from different types of habitat.

	Permanent standing water		Transient ground pools	Container habitats								
	1	2	3	4	5		6	7	8	9	10	11
	Large bodies of water; spring-fed reservoir	Sunken pools and wells	Small pools in ground	Artificial pools, troughs, tanks	Rock pools		Tree holes	Fallen coconuts	Fallen coconut spadix-sheaths	Fallen leaves and palm rachides	Pitchers of *Nepenthes*	Crab-holes
					Exposed	Shaded						
Number from which collections were made	1	4	3	6	8	3	6	2	7	11	2	—
Uranotaenia pandani ..				1					7	10		
U. nepenthes											2	
U. browni										2		
Aëdes vigilax ssp. *vansomerenae*		1	1		2							
Aë. albopictus				4		3	6	2	2			
Aë. pembaensis												+?
Culex simpsoni	1	3	1	3	7							
C. pipiens ssp. *fatigans* ..		1	1				1					

The larval habitats studied may be classified as shown in Table I. This follows Bates's system (1949) as nearly as possible, but running water habitats are omitted because they never produced any mosquitos. This may be partly because owing to the precipitous nature of the islands, running water is largely torrential, and tends to fluctuate violently with weather conditions. As Harper pointed out, however, there are seepage areas, considerable in number if not in extent, which might provide suitable breeding places for species like *Anopheles gambiae* if such occurred.

A classified enumeration of habitat types studied now follows, with a discussion of the species predominating in each.

Permanent standing-water habitats.

1. *Large bodies of water, reservoirs.*—Apart from the large marshes in the coastal flats, in which mosquito larvae were never found, the only habitats of any size are a few scattered reservoirs of moderate dimensions. From egg-rafts collected on one of these (at Grande Anse, Mahé), larvae of *Culex simpsoni* subsequently hatched.

2. *Small sunken pools and wells.*—Those ground pools which were sunk below ground level and appeared more stable, are included here with wells, although it was sometimes difficult to distinguish between temporary and permanent pools. Wells are not uncommon on the flat coral islands where there are no streams, and wells are sunk down to the water table, which may be only a few feet below the surface. A more thorough investigation of these might yield interesting results. Three species were recorded, *Culex simpsoni* (3 records), *C. pipiens fatigans* (1 record) and *Aëdes vigilax vansomerenae* (1 record).

Transient ground pools.

3. *Small pools in ground.*—These are uncommon, produced usually by heavy rainfall, but often also by the incomplete drying out of marshes (Pl. II, fig. 1). There are not enough records (collections were obtained from three only) to make a detailed analysis possible; the same three species were recorded as in (2) above, each species once only.

Container habitats.

Although it is doubtful whether these are homogeneous enough to be distinguished collectively from other types of habitat, they are here treated in this way for convenience. They are by far the most numerous and important in the Seychelles, and altogether records were obtained for 45. They may be grouped as follows.

4. *Artificial pools, troughs and tanks.*—Collections were made from six habitats, including concrete troughs, a rain-water tank, an iron drum and an enamel dish of water frequently left on the verandah for this purpose. Species found were *Aëdes albopictus* (4 records), *Culex simpsoni* (3 records) and *Uranotaenia pandani* (1 record); this is an unusual habitat for the last-named species. *Aë. albopictus* was recorded twice in the enamel dish, and once in the rain-water tank, which was indoors. *C. simpsoni* occurred in the iron drum, and twice in outdoor concrete pools, in all cases in very large numbers.

5. *Rock pools.*—Collections from eleven rock pools included three species: *C. simpsoni* (7 records), *Aë. albopictus* (4 records) and *Aë. vigilax vansomerenae* (2 records). Accumulations of rain water are numerous in depressions in the extensive exposures of granite which form a very characteristic feature of the granitic islands. Some of these pools are close to the sea (Pl. I, fig. 1) and others on higher ground inland (Pl. I, fig. 2). However, the only distinction which appeared to be significant from the point of view of the mosquito fauna was between pools which were shaded, and those which were exposed to the sun

most or all of the time. The latter often became very warm, the temperature rising to as much as 50°C. without apparent harm to the larvae. All the records from exposed pools were of *C. simpsoni* (7) and *Aë. vigilax vansomerenae* (2), while the three shaded pools yielded only *Aë. albopictus*. One of the latter was a small hole drilled in a rock preparatory to blasting it. The shaded pools therefore, as we shall see, have more in common with tree holes than with exposed rock pools (see Garnham, Harper & Highton, 1946).

6. *Tree holes.*—Four of the six tree holes from which collections were obtained were in the bases of the trunks of coconut palms; the remaining two were in trunks of " bois blanc " (*Hernandia ovigera*) on Ile Platte. All of them produced *Aë. albopictus*, which seems to be the principal tree-hole species of the islands. One of the holes in coconut palms produced also *C. pipiens fatigans*. Harper (1947) recorded *Culex stellatus* from the steps cut in the trunks of coconut palms, but these do not frequently contain water and no collections were made from them, although the large holes at the bases probably in some cases developed from these steps.

The next three categories of container habitats are formed by various parts of palms and trees which fall to the ground and are of such shape and size as to hold rain water.

7. *Fallen coconuts.*—Immature coconuts are frequently, although locally, attacked by rats (*Rattus rattus*), which eat a hole in the base of the nut and cause its premature fall. If the nut comes to rest on the ground with the hole upwards (Pl. II, fig. 3), it may collect rain water, which together with any residue of " milk " or endosperm already in the nut forms a fluid richly charged with organic matter and frequently stained deep brownish. Although not quantitatively an important habitat, mosquitos occasionally breed in these nuts. The only two collections made (one of them taken from several nuts) contained only *Aë. albopictus*; this is not surprising, since the high organic content of the water must have much in common with that of the water in tree holes. Thienemann (1950) gives an account of the breeding of mosquitos and other insects in coconuts which have fallen due to similar action by squirrels.

8. *Fallen spadix-sheaths of coconuts.*—The boat-shaped sheaths fall off after the inflorescences have opened, and often collect up to a litre or more of water (Pl. I, fig. 3). Collections obtained from seven sheaths all contained *Uranotaenia pandani* as the principal species, and two of them contained *Aë. albopictus* in addition.

9. *Fallen leaves of palms and trees.*—The rachides of several species of palms are of size and shape suitable for retaining rain water. The large rachis of the coconut palm has numerous separate paired leaflets, each with the lamina depressed on either side of the midrib, so that if the rachis falls lower side upwards each leaflet forms a boat-shaped container. Each palm sheds about one rachis per month, so that a heavy rain rapidly brings into existence very large numbers of larval habitats. The rachides of the double coconut, *Lodoicea maldivica*, and of the palm, *Stevensonia borsigiana*, are undivided except at the margin, so that each may, if it comes to rest suitably on falling, form a container capable of holding a considerable volume of water (Pl. I, fig. 4). Large-leaved dicotyledonous trees may also occasionally produce breeding places in this way, and larvae were obtained from leaves of banana and of *Terminalia catappa*. Of eleven collections, ten contained *Uranotaenia pandani*. The only other species was *U. browni*, collected on two occasions (once with *U. pandani*) from leaves of *Lodoicea* in the remarkable Vallée de Mai on Praslin (Pl. III); this valley carries a forest of these remarkable palms, of which it is almost the only remaining natural home.

These last two categories—fallen leaves and fallen spadix-sheaths, are very similar, and differ from the fallen coconuts in the comparative freedom from dissolved organic matter, which may explain the scarcity of *Aë. albopictus*. Although they provide one of the most abundant and wide-spread habitats, however, they are little used by biting species, and it is doubtful whether the practice of overturning them, as carried out by some planters, is worth while but more extensive investigation would be necessary to confirm this.

10. *Pitchers of* Nepenthes.—*Nepenthes pervillei* is a rare endemic plant, restricted to Mahé and Silhouette and for the most part to the damp forests of the higher mountains. The pitchers (Pl. II, fig. 4) contain a fairly clear fluid of a syrupy consistency, in which most insects are killed and digested, but in which the immature stages of *Uranotaenia nepenthes* can survive.

Two stands of *Nepenthes* were examined in Silhouette and one in Mahé. One of those in Silhouette was extensive, at over 2,000 ft. along the ridge between Mt. Pot-à-eau and Mt. Catherine; here almost every pitcher contained numbers of larvae and large samples were collected and some adults reared from them. The other was on the summit of Mt. Congoment (2,046 ft.); here there were holes eaten out of the base of nearly every pitcher, probably by rats, and the fluid had run out; few mosquito larvae were obtained. The only stand in *Nepenthes* visited in Mahé was at a moderate altitude (about 1,000 ft.) at Sans Souci, and quite isolated from any other *Nepenthes*. Holes had been eaten in many of the pitchers here also, and no larvae were found. *Nepenthes* is stated to occur also at certain stations at high altitudes in Mahé, but these were not visited.

11. *Crab-holes.*—This habitat is included here because although no larvae were ever found in them in the Seychelles, they are almost certainly used by at least one species of mosquito. Semi-terrestrial crabs of the genus *Sesarma* are very abundant in marshy coastal areas. The burrows are found along the margins of drainage ditches (Pl. II, fig. 2) or anywhere where the water table is not too far below ground level for them to reach it. Another larger crab, *Cardisoma carnifex* (Herbst) is found in smaller numbers in similar situations and sometimes in drier areas also.

Aëdes pembaensis almost certainly breeds in these crab-holes and it has been recorded as breeding in them before (Hopkins, 1952). Although larvae were never actually found, few burrows were dug out and examined. The adult mosquitos were very abundant in the coastal marsh areas of Praslin (*e.g.*, Grande Anse and Saint Sauveur) where the crabs were especially numerous and the water often saline, and were frequently to be seen hovering in the mouths of the tunnels. The only other extensive breeding place here was the open water of the marshes themselves and, although it was frequently examined, no larvae were ever found. An average concentration of crab-holes is about three per square yard, but along the banks of waterways it may reach as much as nine per square yard. It will thus be appreciated that they can provide an important breeding place for one of the worst biting species, and in view of the fact that the crabs themselves are of importance as agricultural pests, there may be a case for considering the question of bringing them under control locally. A more complete investigation into the breeding habits and distribution of the mosquito should, however, be undertaken first.

We can summarise the data on breeding places by dividing the mosquitos into three categories:—

1. *Species with a specialised breeding place, the range of which is restricted.*—Here we can include *Uranotaenia nepenthes*, which is probably almost entirely restricted to the high mountains where *Nepenthes* is found, although one should not overlook the fact that Harper (1947) found it in leaf axils. Possibly *Aëdes pembaensis* should be included here, if it is proved that it breeds mainly in crab-holes; it is possible, however, that it has other breeding places. Wiseman & others (1939) record it mainly from crab-holes in the

Mombasa area, but also commonly from pools, puddles, springs, seepages and other habitats. Adults were biting in numbers in the Vallée de Mai on 25th May 1952 some two miles inland, where crab-holes are rare or absent, although there are streams and seepages where they might breed; on the other hand, these adults may have flown inland from the coast. The breeding place of *Taeniorhynchus uniformis* was never found, but if the larvae are restricted to any particular species of plant for respiratory purposes (Hopkins, 1952, p. 111), this species may also be included in this category.

2. *Species with a specialised breeding place which is generally distributed.—Uranotaenia pandani* is largely restricted to fallen leaves and coconut spadix-sheaths for breeding, but these are generally distributed over the islands. Its range is therefore wider than that of *U. nepenthes* (Table II). Although it was

TABLE II.

Island distribution of mosquitos in the Seychelles group, as indicated by the collections studied in this paper and all earlier published records.

	Praslin Group						Silhouette	Mahé Group							Coral Islands		
	Praslin	Cousin	Aride	Grande Soeur	Félicité	Round	Silhouette	Mahé	Sainte Anne	Long	Round	Cerf	Anonyme	Thérèse	Bird	Dennis	Platte
Uranotaenia pandani ..	+			+	+	+		+				+	+				
U. nepenthes ..							+	+									
U. browni	+																
Taeniorhynchus uniformis	+							+?									
Aëdes vigilax ssp. *vansomerenae*							+								+	+	
Aë. aegypti								+									
Aë. albopictus ..	+	+				+	+	+	+	+	+	+	+		+	+	+
Aë. pembaensis ..	+							+									
Aë. albocephalus ..							+	+							+	+	
Culex stellatus ..	+							+									
C. simpsoni	+	+	+		+		+	+	+		+		+	+	+		
C. pipiens ssp. *fatigans*	+				+		+	+	+				+				+
C. scotti	+						+	+									

It should be noted that collecting on islands apart from Mahé and Praslin was only casual, so that the records by no means indicate their complete mosquito fauna.

never found except on the granitic islands, there seems no reason why it should be restricted to them.

3. *Species with varied breeding places, of wide distribution.*—Here one can include *Aëdes albopictus* and *Culex simpsoni*, and possibly also *C. pipiens fatigans* and *Aëdes vigilax vansomerenae*. *Aë. albopictus* seems to prefer shaded habitats with much organic matter and detritus, which allows a fairly wide latitude in choice of habitat (Table I). *C. simpsoni* is largely associated with rock pools, but may breed also in other types of pools. *C. pipiens fatigans* and *Aë. vigilax vansomerenae* were not found frequently enough to draw any general conclusions, but such evidence as there is suggests that the former resembles *Aë. albopictus* and the latter *C. simpsoni*. The type form of *Aë. vigilax* in Australia is stated to breed principally in tidal marshes and pools, and one of the habitats of ssp. *vansomerenae* (on Dennis I.) answers more or less to this type (Hill, 1922; Cooling, 1924*b*).

For the remaining species, evidence is either lacking altogether or quite inadequate to draw any conclusions.

Island Distribution.

The distribution on individual islands within the Seychelles group is shown in Table II, in which both published and new records are included. Good maps of the area for reference have been given by Scott (1933, Pls. 17 and 18).

As previously pointed out, the islands are of two kinds, granitic and coral. Only Bird I., Dennis I., and Ile Platte belong to the latter category, since the outlying groups (Aldabra, Amirantes, etc.) are not included.

There is little to say about this distribution. Certain species are not recorded from coral islands, although there seems no good reason why they should not be except in the case of *Uranotaenia nepenthes*. There is no species confined to the coral islands, although *Aëdes vigilax vansomerenae* appears to be more common there.

The most widely distributed species are *Aëdes albopictus*, *Culex simpsoni* and *Uranotaenia pandani*, collected from 13, 11 and 7 islands, respectively. Breeding habitats may be partly responsible for this; the favourite habitat of *C. simpsoni* is exposed rock pools, which are numerous on the extensive exposures of bare rock on the granitic islands; *Aë. albopictus* is catholic in its choice and can make use of a wide range of container habitats; while the principal habitat of *U. pandani* is the fallen rachides of coconuts which are ubiquitously grown on all the islands.

In assessing the value of these observations, it should be borne in mind that, apart from Silhouette, Praslin and Mahé, collections from individual islands were mostly casual, and make no pretence at being representative of the complete fauna.

Biting Habits.

When biting was conspicuous, samples of adults were frequently collected and notes of the circumstances recorded.

Six species in all were observed to bite, but only two at all frequently. These were *Aëdes albopictus* and *Aë. pembaensis*. Both of these species are outdoor biters, being very abundant in the coconut plantations of the coastal flats; on only one or two occasions was biting noted on the verandah or indoors. *Aë. albopictus* is more widespread, while *pembaensis* is largely restricted to marshy, often rather saline areas, where it is sometimes extremely abundant. Both may bite throughout the day from early morning until dusk, but whereas *albopictus* is almost equally persistent throughout the day, *pembaensis* usually does not make its presence felt until about 3 or 4 p.m., after which the marshy areas of the coastal flats of Praslin become almost intolerable through its attacks. Both species attack the legs principally, but frequently the arms also. Sometimes when *albopictus* females were biting, males were seen to hover around them in attendance, and on one occasion coupling was observed on the wing.

Taeniorhynchus uniformis was taken only twice, a single female in each case, biting on the verandah at dusk.

Aëdes albocephalus was taken biting on Bird I. and Dennis I.; on the latter it attacked indoors about 5.30–6.0 a.m.

The two principal *Culex* species (*C. simpsoni* and *C. pipiens fatigans*) were rarely found biting, but they appear to be the main domestic species. When I awoke one morning a number of mosquitos were found resting on the inside of the mosquito net, which they had evidently entered through a small hole during the night. They were mostly *C. simpsoni*, which were heavily gorged with blood; there was one *C. pipiens fatigans*, but this showed no clear evidence of having fed.

The type form of *Aëdes vigilax* is described as a vicious biter in Australia (Hill, 1922; Cooling, 1924*a*); although no records were obtained of the ssp. *vansomerenae* biting in the Seychelles, this may be due only to its relative scarcity.

Summary.

A list is given of all the species of mosquitos so far recorded from the Seychelles, with their distribution in so far as this is known. A number of new records are included based on collections made recently by one of us (E.S.B.).

One species and one subspecies new to science are here described for the first time. The first full descriptions of the male terminalia and pupae of certain other species are included.

Some notes are given regarding the taxonomy, bionomics and local distribution of the species concerned and the zoogeography of the groups to which they belong.

Appendices are devoted to corrections to the second edition of "The Mosquitoes of the Ethiopian Region", Vol. I by G. H. E. Hopkins, and to the mosquitos of other islands in the western Indian Ocean.

Appendix I.

The Mosquitos of other Islands in the western Indian Ocean.

1. THE CHAGOS ARCHIPELAGO.

The only record is of *Aëdes albopictus* from Peros Banhos Atoll (Diamant I., as *scutellaris*, 19.v.1905; Theobald, 1912). These islands lie between the Seychelles and the southern tip of Sumatra. The record thus does nothing to support the suggestion of a land connection with India although it is consistent with a direct entry into the Seychelles from the Malayan sub-region.

2. THE AMIRANTE ISLANDS.

Edwards (1941) states that there are no records from these islands. This is untrue. Theobald (1912) gives records of *Aë. aegypti* (as *Stegomyia fasciata* F., Darros I., 13.x.1905) and *Aë. albopictus* (as *scutellaris*, Desroches I., 15.viii.1905). The specimen of *Aë. aegypti* on which the record is based is in the British Museum. It apparently belongs to the type form.

3. THE ALDABRA AND COSMOLEDO GROUPS.

Theobald (1912) gives records of *Aë. aegypti* (as *fasciata*, Picard I., 1908–1909, coll. *J. C. F. Fryer*), *Aë. albocephalus* (as *R. seychellensis*, Takamaka, 1908–1909. coll. *Fryer*) and *Aë. fryeri* (as *Culicelsa fryeri* sp. n., Takamaka, 1908–1909, coll. *Fryer*) from the Aldabra group and Edwards (1941) has a record of *Aë. fryeri* from Cosmoledo I. as well as another from Aldabra (both coll. *Dupont*). The British Museum has a series of *Culex sitiens* Wied. from Aldabra (coll. *Dupont*, circa 1907) which does not appear to have been published previously. It is remarkable that this widespread species has not been found in the Seychelles proper. Hermitte (1931) records *Anopheles gambiae* for the first and only time from Aldabra (coll. *J. T. Bradley*, 1930). This is one of the few species of mosquito known with certainty to be susceptible to human introduction and it would appear that its presence was very probably due to this agency. The zoogeography of *Aë. fryeri* and its relatives has been discussed above. Of the *Aë. aegypti* an isolated specimen in the British Museum from Aldabra appears to be of the type form while a small series from Picard I. conforms to var. *queenslandensis*.

4. COETIVY ISLAND.

Theobald (1912) gives a record of *Aë. albopictus* (as *scutellaris*, 10.v.1905).

5. THE COMORO ISLANDS.

Edwards (1941) gives a record of *Aë. aegypti* based on larvae from Grand Comoro in the Paris Museum (coll. *Pobeguin*, 1899). The Paris Museum also has larvae of *Culex fatigans* and a single whole larva apparently of *Culex theileri* Theo. (both coll. *Pobeguin*). Ventrillon (1905, 1906) records *Eretmapodites quinquevittatus* Theo. (as *E. condei*, n. sp.) and *Aë. pembaensis* (as *Stegomyia cartroni*, n. sp.), respectively, from Mayotte I. The record of *Culex theileri* is of particular interest. Monsieur Séguy was kind enough to lend me the larva so that I was able to examine it thoroughly. This species is widely distributed from the Canary Islands along both sides of the Mediterranean eastwards through Irak, Iran, Baluchistan and N.W. India and along the Himalayan foothills into northern Burma and Assam. It is common in the Yemen and has been found on Jebel Jihaf. On the African mainland it extends southwards from Egypt through the Sudan, Abyssinia and Eritrea to the Kenya highlands, thence by the central plateau to reach the coast in Natal and westwards through Cape Province into S.W. Africa. It has not been found in the coastal lowlands of east Africa (*fide* E. C. C. van Someren) although those of Kenya have recently been rather thoroughly collected. (See the remarks on Zanzibar in Appendix I.) *Eretmapodites quinquevittatus*, on the other hand, is well known to occur in the eastern lowlands. This species occurs in Zanzibar but, so far as is known, *C. theileri* does not. Neither species is known from Madagascar.

6. BASSAS DA INDIA GROUP.

Doucet (1950) has a record of *Eretmapodites plioleuca* Edw. from Europa I. The same author (*l.c.*) records this species from Madagascar but as it is known elsewhere only from west and central Africa the record would seem to require confirmation.

7. MADAGASCAR.

Doucet (1950, 1951*a*,*b*) records 84 species of Culicini and De Meillon (1947) records 16 species of Anophelini, Doucet (1951*c*) has added one and Grjebine (1953) five new species of *Anopheles*, and the latter has added five new species of Culicini. This is a large increase on the five species of Anophelini and 25 species of Culicini recorded by Edwards (1941). A detailed analysis of the fauna must await the discovery of adults of the numerous species which have so far been recorded from the early stages only.

8. THE MASCARENES.

MacGregor (1924, 1927) recorded 4 species of Anophelini and 17 species of Culicini from Mauritius. Gebert (1948) added a new endemic species of *Aëdes* (*Mucidus*) and Mattingly (1953*a*) a new endemic *Stegomyia*. Early records from Réunion (Blanchard, 1902) are difficult to interpret and Edwards (1920) records only two species. Nevertheless from these records and from material kindly sent by Monsieur Hamon it seems clear that the following species occur:—

Anopheles coustani Lav., *A. gambiae* Giles, *Aëdes fowleri* (Charmoy), *Aë. aegypti* (L.), *Aë. albopictus* (Skuse), *Culex tigripes* Grandpré & Charmoy, *C. insignis* (Carter), *C. tritaeniorhynchus* Giles, *C. poicilipes* (Theo.), *C. pipiens* ssp. *fatigans* Wied.

Information regarding some of these species will be found in Hamon & Dufour (1952). In addition, Hamon (1953*a*) has recently added the new species of *Ochlerotatus* which is discussed above. The mosquitos of these islands cannot be discussed in detail here. From a zoogeographical point of view the most interesting of them is perhaps *Orthopodomyia arboricolis* (Charmoy) which is apparently endemic in Mauritius. Two other endemic species of this genus occur in Madagascar and another, the first from the African mainland, has recently been found in Cape Province (J. Muspratt, *in litt.*). This very interesting genus occurs in the Oriental and Palaearctic regions, in New Guinea and in both Americas. In view of its almost total absence from the mainland of Africa, the comparison with *Ochlerotatus* is interesting.*

9. ZANZIBAR, MAFIA AND PEMBA.

An analysis of the fauna of these islands can probably be more usefully made after publication of a survey of the mosquitos of the Kenya lowlands which is understood to be in preparation (E. C. C. van Someren, *in litt.*). An interesting point is the occurrence on them of a number of species occurring wholly or mainly in the highlands of the adjacent East African territories. This may reflect the very sharp temperature gradient characteristic of small islands, a factor which certainly has a profound effect on the local distribution of mosquitos on such islands (Jepson, Moutia & Courtois, 1947; Mattingly, 1953*a*). For a faunal list of the mosquitos of these islands see Edwards (1941).

10. JUAN DE NOVA.

Specimens of *Culex pipiens fatigans* have kindly been sent by Monsieur Hamon.

11. SOCOTRA.

A full list of mosquitos will be found in Leeson & Theodor (1948). The fauna includes a very interesting endemic *Stegomyia*, *Aëdes granti* (Theo.), with Indo-Australian affinities (Mattingly, 1953*a*). Apart from this the mosquitos are mainly Arabian in their affinities.

12. MALDIVE AND LACCADIVE GROUPS.

Iyengar (1952) listed 13 species from the Maldives. Two more species are added in a further paper by Iyengar & Menon (1955).

---

* For information concerning mosquitos of the Mascarenes which has come to hand since this note was written see Halcrow (1954*a*, *b*), Hamon (1953*b*) and Mattingly & Bruce-Chwatt (1954).

APPENDIX II.

Proposed Corrections to the Key to Larvae of *Culex* (Hopkins, 1952).

By P. F. MATTINGLY.

The error of observation noted above in connection with Hopkins' description of the larva of *Culex simpsoni* necessitates an amendment to his key (p. 247). The larva of *Culex zombaensis* Theo. is still not known to me from associated skins but I have whole larvae from Abyssinia which almost certainly belong to this species. Since it comes into the same section of the key as *C. simpsoni* I have taken the opportunity to make further amendments to this section. The amended key should read as follows:—

28. Comb composed of spines only; head setae B and C with 3 and 3–4 branches respectively .... *theileri* (p. 289).
Either with comb composed partly of scales or with head setae B and C at most double or both .... 29.

29. Head setae B and C each with at least 3 branches ... *zombaensis* (p. 306).
These setae with at most 2 branches .... 29*a*.

29*a*. Siphonal index about 9; mentum with about 9 teeth on each side of the central tooth; pecten extending to about 1/6th .... *kingianus* (p. 255).
Siphonal index at most 7½, usually less; mentum with 4–5 teeth on either side of the central tooth; pecten extending to at least 1/4th .... 30.

30. Siphonal index 4½ .... *seldeslachtsi* (p. 298).
Siphonal index about 6–7 .... 31.

31. Pecten extending to about 2/5ths .... *sinaiticus* (p. 293).
Pecten extending to less than 1/3rd .... *simpsoni* (p. 295).

At the end of the key couplet 65 should be deleted and "*univittatus* (p. 291)" should be substituted for "65." in the second half of couplet 64.

References.

BAISAS, F. E. (1935). Notes on Philippine mosquitoes, II. *Uranotaenia* group.—Philipp. J. Sci., **57**, pp. 63–80.

BAISAS, F. E. & UBALDO-PAGAYON, A. (1952). Notes on Philippine mosquitoes, XVI. Genus *Tripteroides*.—Monogr. Inst. Sci. Tech. Philipp., no. 2, 198 pp.

BARRAUD, P. J. (1934). The fauna of British India . . . Diptera. Vol. V. Family Culicidae. Tribes Megarhinini and Culicini.—463 pp. London, Taylor & Francis.

BATES, M. (1949). The natural history of mosquitoes.—379 pp. New York, Macmillan.

BELKIN, J. N. (1950). A revised nomenclature for the chaetotaxy of the mosquito larva (Diptera: Culicidae).—Amer. Midl. Nat., **44**, pp. 678–698.

BELKIN, J. N. (1952). The homology of the chaetotaxy of immature mosquitoes and a revised nomenclature for the chaetotaxy of the pupa (Diptera, Culicidae).—Proc. ent. Soc. Wash., **54**, pp. 115–130.

BELKIN, J. N. (1953*a*). Mosquitoes of the genus *Uranotaenia* in the Solomon Islands (Diptera: Culicidae).—Pacif. Sci., **7**, pp. 312–391.

Belkin, J. N. (1953*b*). Corrected interpretations of some elements of the abdominal chaetotaxy of the mosquito larva and pupa (Diptera. Culicidae).—Proc. ent. Soc. Wash., **55,** pp. 318–324.

Belkin, J. N. (1954). The dorsal hairless setal ring of mosquito pupae (Diptera: Culicidae).—Pan-Pacif. Ent., **30,** pp. 227–230.

Blanchard, R. (1902). Note sur les moustiques de la Réunion.—C.R. Soc. Biol., **54,** pp. 643–644.

Blanchard, R. (1905). Les moustiques . . .—673 pp. Paris.

Bohart, R. M. & Ingram, R. L. (1946). Mosquitoes of Okinawa and islands in the central Pacific.—NAVMED, no. 1055, 110 pp. Washington, D.C., Bur. Med. Surg., Navy Dep.

Bonne-Wepster, J. (1934). New mosquitos (Dipt.) from the Netherlands Indies.—Stylops, **3,** pp. 272–276.

Bonne-Wepster, J. & Brug, S. L. (1932). The subgenus *Stegomyia* in Netherland India.—Geneesk. Tijdschr. Ned.-Ind., Bijblad, no. 2, pp. 35–119.

Brug, S. L. (1924). Notes on Dutch-East-Indian mosquitos.—Bull ent. Res., **14,** pp. 433–442.

Brug, S. L. (1931*a*). Culiciden der Deutschen Limnologischen Sunda-Expedition.—Arch. Hydrobiol., Suppl. 9, pp. 1–42.

Brug, S. L. (1931*b*). New Culicidae from Sumatra.—Tijdschr. Ent., **74,** pp. 245–250.

Brug, S. L. (1939). Notes on Dutch East-Indian mosquitoes.—Tijdschr. Ent., **82,** pp. 91–113.

Brug, S. L. & Bonne-Wepster, J. (1947). The geographical distribution of the mosquitoes of the Malay Archipelago.—Chron. nat., **103,** pp. 179–197.

Callot, J. (1940). Sur quelques moustiques du Maroc.—Arch. Inst. Pasteur Maroc, **2,** pp. 361–365.

Carter, H. F. & Wijesundara, D. P. (1948). Notes on some Ceylon Culicine mosquitoes.—Ceylon J. Sci., (B) **23,** pp. 135–151.

Christophers, S. R. (1933). The fauna of British India . . . Diptera. Vol. IV. Family Culicidae. Tribe Anophelini.—371 pp. London, Taylor & Francis.

Cooling, L. E. [1924*a*]. Seven common species of mosquitoes described for purposes of identification.—Serv. Publ. Dep. Hlth Aust. trop. Div., no. 1, 24 pp.

Cooling, L. E. [1924*b*]. The larval stages and biology of the commoner species of Australian mosquitoes. . . .—Serv. Publ. Dep. Hlth Aust. trop. Div., no. 8, 40 pp.

De Beer, G. R. (1951). Embryos and ancestors. 2nd edn. Oxford.

De Meillon, B. (1947). The Anophelini of the Ethiopian geographical region.—Publ. S. Afr. Inst. med. Res., no. 49, 272 pp.

Dobrotworsky, N. V. & Drummond, F. H. (1953). The *Culex pipiens* group in south-eastern Australia. II.—Proc. Linn. Soc. N.S.W., **78,** pp. 131–146.

Doucet, J. (1949*a*). Etude des Culicidae (Diptera) du Lac Alaotra, II.—Mém. Inst. sci. Madagascar, (A) **3,** pp. 121–145.

Doucet, J. (1949*b*). Recherches sur les Culicides de Madagascar.—Mém. Inst. sci. Madagascar, (A) **3,** pp. 325–332.

DOUCET, J. (1950). Les Culicinés de Madagascar (Dipt.).—Mém. Inst. sci. Madagascar, (A) **4,** pp. 39–65.

DOUCET, J. (1951*a*). Les moustiques de la région de Perinet.—Mém. Inst. sci. Madagascar, (A) **6,** pp. 63–82.

DOUCET, J. (1951*b*). Etude des Culicides de la région de Vangaindrano (Diptera).—Mém. Inst. sci. Madagascar, (A) **6,** pp. 83–114.

DOUCET, J. (1951*c*). Les Anophélinés de la Région Malgache.—Publ. Inst. Rech. sci. Tananarive-Tsimbazaza, 198 pp.

EDWARDS, F. W. (1912). A synopsis of the species of African Culicidae, other than *Anopheles*.—Bull. ent. Res., **3,** pp. 1–53.

EDWARDS, F. W. (1914*a*). New species of Culicidae in the British Museum, with notes on the genitalia of some African *Culex*.—Bull. ent. Res., **5,** pp. 63–81.

EDWARDS, F. W. (1914*b*). New Culicidae from Borneo and Hong Kong.—Bull. ent. Res., **5,** pp. 125–128.

EDWARDS, F. W. (1915). Diagnoses of new Bornean Culicidae.—Bull. ent. Res., **5,** pp. 283–285.

EDWARDS, F. W. (1920). Notes on the mosquitos of Madagascar, Mauritius and Réunion.—Bull. ent. Res., **11,** pp. 133–138.

EDWARDS, F. W. (1921). A revision of the mosquitos of the Palaearctic Region.—Bull. ent. Res., **12,** pp. 263–351.

EDWARDS, F. W. (1925). Mosquito notes. V.—Bull. ent. Res., **15,** pp. 257–270.

EDWARDS, F. W. (1926). Mosquito notes. VI.—Bull. ent. Res., **17,** pp. 101–131.

EDWARDS, F. W. (1932). Diptera. Fam. Culicidae.—Genera Insect., **194,** 258 pp. Brussels, Wytsman.

EDWARDS, F. W. (1935). Mosquito notes. XII.—Bull. ent. Res., **26,** pp. 127–136.

EDWARDS, F. W. (1941). Mosquitoes of the Ethiopian Region. III. Culicine adults and pupae.—499 pp. London, Brit. Mus. (Nat. Hist.).

FARNER, D. S., DICKE, R. J., SWEET, G., ISENHOUR, L. & HSIAO, T. Y. (1946). The distribution of mosquitoes of medical importance in the Pacific area.—NAVMED no. 983, 64 pp. Washington, D.C., Bur. med. Surg., Navy Dep.

GARNHAM, P. C. C., HARPER, J. O. & HIGHTON, R. B. (1946). The mosquitos of the Kaimosi Forest, Kenya Colony, with special reference to yellow fever.—Bull. ent. Res., **36,** pp. 473–496.

GEBERT, S. (1948). Notes on a new species of *Aëdes*, sub-genus *Mucidus* (Diptera: Culicidae) found in Mauritius.—Entomologist, **81,** pp. 96–99.

GRJEBINE, A. (1953). Observations sur les Nématocères vulnérants de Madagascar, régions de Majunga et de la Mandraka.—Mém. Inst. sci. Madagascar, (E) **4,** pp. 443–502.

HADDOW, A. J. (1948). The mosquitoes of Bwamba County, Uganda. VI. Mosquito breeding in plant axils.—Bull. ent. Res., **39,** pp. 185–212.

HALCROW, J. G. (1954*a*). Occurrence of *Culex simpsoni* in Mauritius.—Nature, Lond., **174,** p. 466.

HALCROW, J. G. (1954*b*). Catalogue of the mosquitoes of Mauritius and Rodrigues.—Mauritius Inst. Bull., **3,** pp. 234–248.

HAMON, J. (1953*a*). Une nouvelle espèce d'*Aëdes* de l'Île de la Réunion (Diptère Culicidae).—Nat. malgache, **5**, pp. 35–41.

HAMON, J. (1953*b*). Etude biologique et systématique des Culicidae de l'Île de la Réunion.—Mém. Inst. sci. Madagascar, (E) **4**, pp. 521–541.

HAMON, J. & DUFOUR, —. (1952). Rapport sur la lutte antipaludique, campagne 1951–1952.—60 pp. St. Denis, La Réunion.

HARPER, J. O. (1947). A mosquito survey of Mahé, Seychelles.—E. Afr. med. J., **24**, pp. 25–29.

HARRISON, L. (1928). The composition and origins of the Australian fauna, with special reference to the Wegener hypothesis.—Rep. Aust. Ass. Adv. Sci., **18**, pp. 332–396.

HERMITTE, L. C. D. (1931). Occurrence of *Anopheles gambiae* (*costalis*) in Aldabra Islands (Seychelles).—Rec. Malar. Surv. India, **2**, pp. 643–654.

HILL, G. F. (1922). Notes on the habits and distribution of some North Australian Culicidae.—Serv. Publ. Dep. Hlth Aust., no. 21, 40 pp.

HOLDHAUS, K. (1927–28). Die geographische Verbreitung der Insekten.—*In* Schröder C. Handbuch der Entomologie, **2**, pp. 592–1058. Jena.

HOOGSTRAAL, H. & CHAMBERLAIN, R. W. (1946). The larva and male of *Aëdes* (*Skusea*) *amesii* (Ludlow) (Diptera, Culicidae).—Proc. ent. Soc. Wash., **43**, pp. 125–131.

HOPKINS, G. H. E. (1952). Mosquitoes of the Ethiopian Region. I. Larval bionomics of mosquitoes and taxonomy of Culicine larvae.—2nd edn., 355 pp. London, Brit. Mus. (Nat. Hist.).

IYENGAR, M. O. T. (1952). Filariasis in the Maldive Islands.—Bull. World Hlth Org., **7**, pp. 375–403.

IYENGAR, M. O. T. & MENON, M. A. U. (1955). Mosquitos of the Maldive Islands.—Bull. ent. Res., **46**, pp. 1–9.

JEPSON, W. F., MOUTIA, A. & COURTOIS, C. (1947). The malaria problem in Mauritius; the bionomics of Mauritian Anophelines.—Bull. ent. Res., **38**, pp. 177–208.

KING, W. V. & HOOGSTRAAL, H. (1946). Three new species of *Aëdes* from Netherlands New Guinea.—Proc. ent. Soc. Wash., **48**, pp. 95–106.

KIRKPATRICK, T. W. (1925). The mosquitoes of Egypt.—224 pp. Cairo, Egypt. Govt. Anti-Malar. Comm.

KNIGHT, K. L. (1953). The mosquitoes of the Yemen (Diptera, Culicidae).—Proc. ent. Soc. Wash., **55**, pp. 212–234.

KNIGHT, K. L. & HULL, W. B. (1951). The *Aëdes* mosquitoes of the Philippine Islands. I.—Pacif. Sci., **5**, pp. 211–251.

KNIGHT, K. L. & HULL, W. B. (1952). The *Aëdes* mosquitoes of the Philippine Islands. II.—Pacif. Sci., **6**, pp. 157–187.

KNIGHT, K. L. & HULL, W. B. (1953). The *Aëdes* mosquitoes of the Philippine Islands. III.—Pacif. Sci., **7**, pp. 453–481.

KNIGHT, K. L. & ROZEBOOM, L. E. (1946). The *Aëdes* (*Stegomyia*) *albolineatus* group (Diptera, Culicidae).—Proc. biol. Soc. Wash., **59**, pp. 83–98.

LA CASSE, W. J. & YAMAGUTI, S. (1950). Mosquito fauna of Japan and Korea.—3rd edn., 488 pp. [Washington, D.C., Off. Surg. Gen. U.S. Army.]

LANE, J. & CERQUEIRA, N. L. (1942). Os Sabetíneos da América (Diptera, Culicidae).—Arq. Zool. S. Paulo, **3**, pp. 473–849.

Lee, D. J. (1944). An atlas of the mosquito larvae of the Australasian region. Tribes Megarhinini and Culicini.—(Issued by the Australian Military Forces.)

Leeson, H. S. & Theodor, O. (1948). Mosquitos of Socotra.—Bull. ent. Res., **39,** pp. 221–229.

Leicester, G. F. (1908). The Culicidae of Malaya.—Stud. Inst. med. Res. F.M.S., **3,** no. 3, pp. 18–261.

MacGregor, M. E. (1924). Report on the Anophelinae of Mauritius. . . .—48 pp. London, Colon. Off.

MacGregor, M. E. (1927). Mosquito surveys. . . .—282 pp. London, Wellcome Bur. sci. Res.

Mackerras, I. M. (1927). Notes on Australian mosquitoes (Diptera, Culicidae). Part ii.—Proc. Linn. Soc. N.S.W., **52,** pp. 284–298.

Mackerras, I. M. (1950). The zoogeography of the Diptera.—Aust. J. Sci., **12,** pp. 157–161.

Marks, E. N. (1949). Studies of Queensland mosquitoes. 4.—Pap. Dep. Biol. Univ. Qd, **2,** no. 11, 41 pp.

Marks, E. N. (1954). A review of the *Aedes scutellaris* subgroup with a study of variation in *Aedes pseudoscutellaris* (Theobald) (Diptera, Culicidae).—Bull. Brit. Mus. (nat. Hist.), Ent., **3,** pp. 49–414.

Mattingly, P. F. (1952). The sub-genus *Stegomyia* (Diptera: Culicidae) in the Ethiopian Region. (Part I).—Bull. Brit. Mus. (nat. Hist.), Ent., **2,** pp. 233–304.

Mattingly, P. F. (1953*a*). The sub-genus *Stegomyia* (Diptera: Culicidae) in the Ethiopian region. (Part II).—Bull. Brit. Mus. (nat. Hist.), Ent., **3,** pp. 1–65.

Mattingly, P. F. (1953*b*). Notes on the Culicini of the Katanga (Diptera, Culicidae). Part I.—Rev. Zool. Bot. afr., **47,** pp. 311–343.

Mattingly, P. F. (1954*a*). The distribution of some African mosquitoes.—Proc. Linn. Soc. Lond., **165,** pp. 49–61.

Mattingly, P. F. (1954*b*). Notes on the subgenus *Stegomyia* (Diptera, Culicidae) with a description of a new species.—Ann. trop. Med. Parasit., **48,** pp. 259–270.

Mattingly, P. F. & Bruce-Chwatt, L. J. (1954). Morphology and bionomics of *Aëdes* (*Stegomyia*) *pseudoafricanus* Chwatt (Diptera, Culicidae) with some notes on the distribution of the subgenus *Stegomyia* in Africa.—Ann. trop. Med. Parasit., **48,** pp. 183–193.

Mattingly, P. F. & others (1951). The *Culex pipiens* complex.—Trans. R. ent. Soc. Lond., **102,** pp. 331–382.

de Meijere, J. C. H. (1910). Nepenthes-Tiere. I. Systematik.—Ann. Jard. bot. Buitenz., suppl. 3, pp. 917–940.

Muspratt, J. (1953). Research on South African Culicini (Diptera, Culicidae) 1.—J. ent. Soc. S. Afr., **16,** pp. 51–58.

Paulian, R. (1950). Les moustiques des *Nepenthes* à Madagascar.—Nat. malgache, **2,** pp. 119–121.

Pittendrigh, C. S. (1950*a*). The ecoclimatic divergence of *Anopheles bellator* and *A. homunculus*.—Evolution, **4,** pp. 43–63.

Pittendrigh, C. S. (1950*b*). The ecotopic specialization of *Anopheles homunculus*. and its relation to competition with *A. bellator*.—Evolution, **4,** pp. 64–78.

REBÊLO, A. & DE CARVALHO PEREIRA, M. (1943). Culicini (Diptera, Nematocera) da colónia de Moçambique. II.—Moçambique, no. 34, pp. 81–90.

SCOTT, H. (1933). General conclusions regarding the insect fauna of the Seychelles and adjacent islands.—Trans. Linn. Soc. Lond., (Zool.) **19,** pp. 307–391.

SENEVET, G., GAUD, J. & MILLET, A. (1949). Validité de l'espèce *Culex mauritanicus* Callot, 1940.—Arch. Inst. Pasteur Algér., **27,** pp. 42–47.

SKUSE, F. A. A. (1889). Diptera of Australia. Part V. The Culicidae.—Proc. Linn. Soc. N.S.W., **3,** pp. 1717–1764.

STONE, A. & ROSEN, L. (1952). A new species of *Aëdes* from Tahiti (Diptera: Culicidae).—Proc. Hawaii. ent. Soc., **14,** pp. 425–428.

THEOBALD, F. V. (1903). A monograph of the Culicidae, or mosquitoes of the World, **3.**—London, Brit. Mus. (Nat. Hist.).

THEOBALD, F. V. (1910). *Ibid.*, **5.**

THEOBALD, F. V. (1911). The distribution of the yellow fever mosquito (*Stegomyia fasciata*, Fabricius) and general notes on its bionomics.—Trans. I. int. Congr. Ent., **2,** pp. 145–170.

THEOBALD, F. V. (1912). The Percy Sladen Trust expedition to the Indian Ocean . . . Culicidae.—Trans. Linn. Soc. Lond., (Zool.) **15,** pp. 81–94.

THIENEMANN, A. (1950). Lebensraum: Lebensbedingung und Lebenshindernis. —Orion, **5,** pp. 417–421.

UVAROV, B. P. (1953). Some effects of past climatic changes on the distribution of African Acrididae.—Trans. IXth int. Congr. Ent., **2,** pp. 157–159.

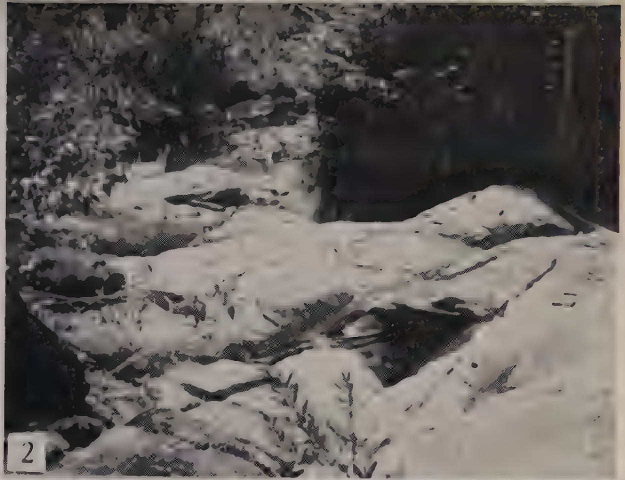
VAN SOMEREN, E. C. C. (1947). The description of a new mosquito from the Seychelles.—E. Afr. med. J., **24,** pp. 29–35.

VENTRILLON, E. (1905). Culicides nouveaux de Madagascar.—Arch. Parasit., Paris, **9,** pp. 441–450.

VENTRILLON, E. (1906). *Stegomyia cartroni*, culicide nouveau de Madagascar.—Bull. Mus. Hist. nat., Paris, **12,** pp. 143–145.

WISEMAN, R. H., SYMES, C. B., MCMAHON, J. C. & TEESDALE, C. (1939). Report on a malaria survey of Mombasa.—60 pp. Nairobi.

WOODHILL, A. R. & PASFIELD, G. (1941). An illustrated key to some common Australian Culicine mosquito larvae, with notes on the morphology and breeding places.—Proc. Linn. Soc. N.S.W., **66,** pp. 201–214.



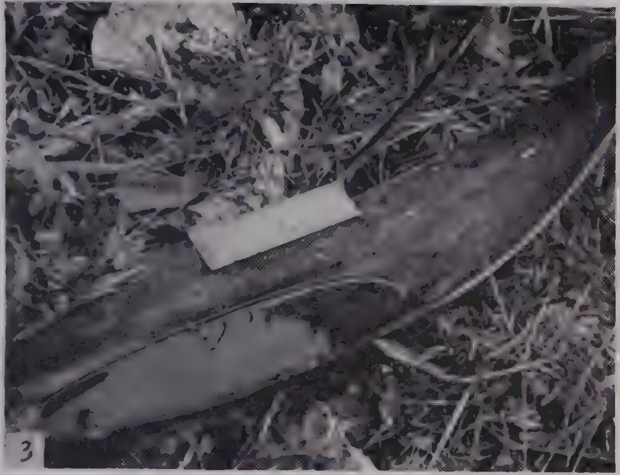
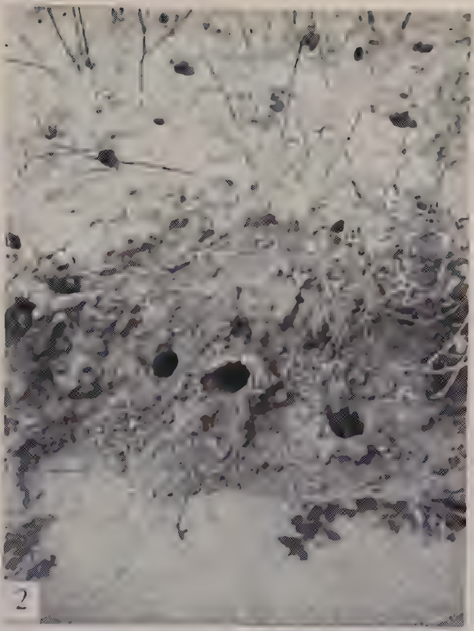
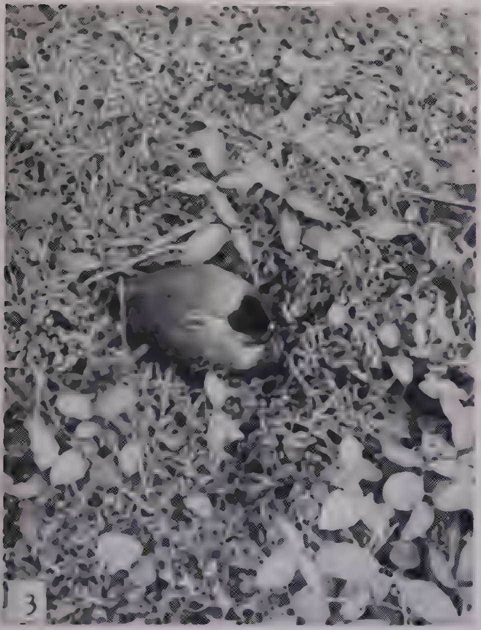


FIG. 1. Exposed rock pool on cliffs near the sea, Silhouette. Breeding place of *Culex simpsoni* and *Aëdes vigilax* subsp. *vansomerenae*.

FIG. 2. Exposed rock pool near stream at about 1,000 ft., Mahé. Breeding place of *Culex simpsoni*.

FIG. 3. Fallen spadix-sheath of coconut. Breeding place of *Uranotaenia pandani*. (The ruler is





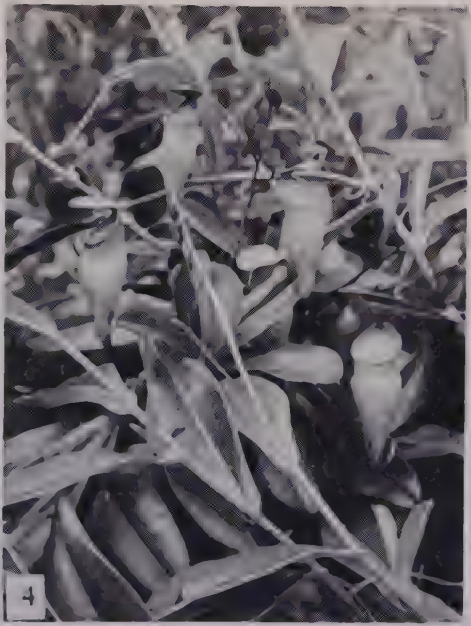
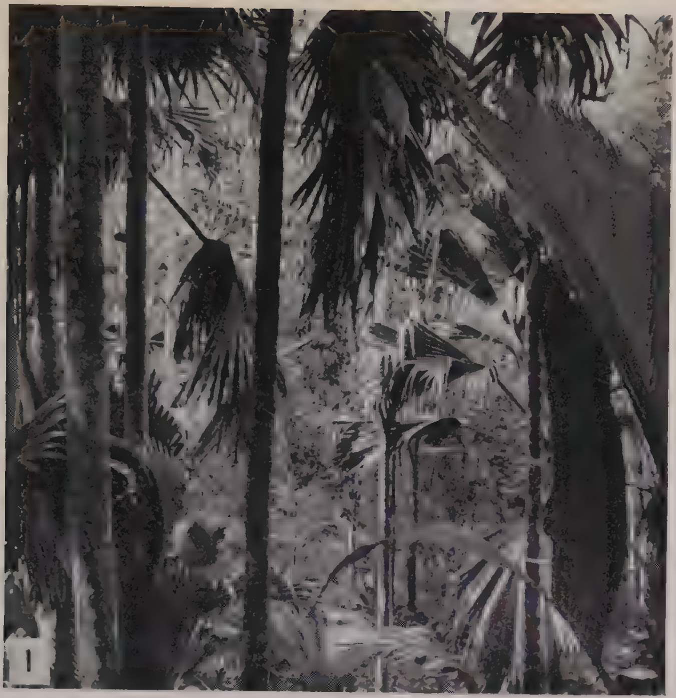


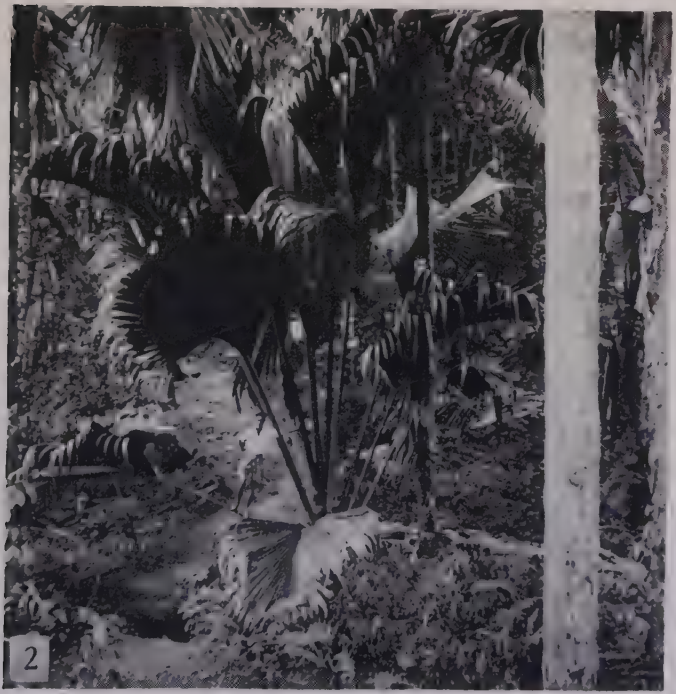
FIG. 1. Ground pool in coastal marsh, Dennis I. Breeding place of *Aëdes vigilax* subsp. *vansomerenae*.

FIG. 2. Burrows of crabs (*Sesarma* sp.). Probable breeding place of *Aëdes pembaensis*.

FIG. 3. Coconut fallen prematurely owing to hole eaten by rat. Breeding place of *Aëdes albopictus*.

FIG. 4. Pitchers of *Nepenthes pervillei*. Breeding place of *Uranotaenia nepenthes*.





Forest of *Lodoicea maldivica* (double coconut, or coco-de-mer).
Habitat of *Uranotaenia browni.*

FIG. 1. View through forest, with trunks of *Lodoicea* and (on right) rachis of *Stevensonia* palm.

FIG. 2. Young *Lodoicea* palm, showing large size of rachides (compare man standing on stalk). The fallen rachides of such broad-leaved palms collect rain water and form important breeding places for mosquitos.

A NOTE ON THE PARASITISATION OF THE OÖTHECAE OF *PERIPLANETA AMERICANA* (L.) BY THE CHALCID, *SYNTOMOSPHYRUM GLOSSINAE* WTSTN.

By T. A. M. Nash, O.B.E., D.Sc. (Lond.)
Chief Entomologist, West African Institute for Trypanosomiasis Research.

Syntomosphyrum glossinae Wtstn. has long been known as a pupal parasite of tsetse flies in East Africa; Nash (1933) found that it will attack the larva as well as the pupa of *Glossina morsitans* Westw. With regard to its other hosts, Lamborn (1925) succeeded in breeding *S. glossinae* in pupae of *Musca nebulo* Patton & Cragg,* *Dacus brevistylus* Bezzi,** and *Chrysomyia putoria* (Wied.); he also found that it was a hyperparasite of *Mutilla glossinae* Turner, which may be attacked in both the larval and pupal stages. Later the list was extended to cover *Chrysomyia marginalis* (Wied.), *C. chloropyga* (Wied.) and *C. albiceps* (Wied.), as well as *Sarcophaga haemorrhoidalis* (Fall.) (Nash, 1933).

In 1947 the writer discovered that *Syntomosphyrum glossinae* also occurs in West Africa, as a pupal parasite of *Glossina palpalis* (R.-D.) in Northern Nigeria (Nash, 1947). In view of this discovery, the strictest measures have been enforced to prevent this parasite from gaining access to the fly-breeding establishment of this Institute where thousands of pupae of *G. palpalis* are bred monthly for experimental purposes. Pupae are all kept under half an inch of sand in containers covered in organdie, a material with a mesh sufficiently fine to exclude even this small parasite. The sand is an additional protection as the parasite cannot penetrate more than one-tenth of an inch into such a soil (Nash, 1933).

In November 1953, great alarm was occasioned by the appearance of large numbers of *S. glossinae* on the *inside* of the windows of the fly-room. Examination of all the pupal containers failed to reveal any parasites or any pupae bearing the tell-tale emergence hole made by the parasite. It was therefore assumed that a few tsetse larvae must have wriggled out of badly made Bruce boxes and have pupated on the floor of the fly-room where they could be readily parasitised. In the search of the floor which was then made, Mallam H. M. Yesufu, Technical Assistant in charge of fly-breeding, with commendable discernment noticed a cockroach oötheca bearing the characteristic emergence hole of the parasite. Further search revealed some 40 parasitised egg capsules, from some of which parasites were in the process of emerging. No tsetse pupae were found on the floor.

Control measures against cockroaches (*Periplaneta americana* (L.)) were mmediately put into force. During the next three months no more *S. glossinae* were seen and no tsetse pupae turned out to be parasitised, which speaks well for the method employed in safeguarding pupae against such a risk.

Twenty-three years ago the writer spent much time investigating this parasite n Tanganyika Territory. He finally worked out an easy technique for breeding t in huge numbers and liberated nearly 14 million parasites in the breeding sites of *G. morsitans*. This experiment in biological control failed because *S. glossinae* s incapable of penetrating sandy soils to a sufficient depth to reach the tsetse pupae (Nash, 1933).

---

* *Musca domestica nebulo* F.—Ed.

** *Dacus ciliatus* Lw.—Ed.

Since the oöthecae of domestic cockroaches are not buried they must be highly vulnerable to attack by *S. glossinae*. It is suggested that this parasite might have possibilities as a means of controlling cockroach infestations in buildings—other than tsetse-breeding establishments.

Summary.

Syntomosphyrum glossinae Wtstn., a Chalcid parasite of the pupae of tsetse flies in East and West Africa, is recorded parasitising the oöthecae of *Periplaneta americana* (L.) at the West African Institute for Trypanosomiasis Research, Kaduna, Northern Nigeria.

References.

Lamborn, W. A. (1925). An attempt to control *Glossina morsitans* by means of *Syntomosphyrum glossinae*, Waterston.—Bull. ent. Res., **15**, pp. 303–309.

Nash, T. A. M. (1933). The ecology of *Glossina morsitans*, Westw., and two possible methods for its destruction.—*Ibid.*, **24**, pp. 107–157, 163–195.

Nash, T. A. M. (1947). A record of *Syntomosphyrum glossinae* from Nigeria.—*Ibid.*, **38**, p. 525.

THE TERMITES OF NORTH-EASTERN TANGANYIKA: THEIR DISTRIBUTION AND BIOLOGY.

By P. Belinda Kemp, M.A.
(*formerly of the Colonial Termite Research Unit*).

(Plates IV–X.)

A detailed study of the termite fauna of north-eastern Tanganyika was made during the period 1950–52. The region concerned covers approximately 11,000 square miles, extending from latitude 4°00′S. to 6°00′S., and from longitude 37°E. to the Indian Ocean. Statements made in the following account refer only to this restricted portion of East Africa.

The region consists of a plain rising gently from sea level to 3,000 feet in the west, with a mountain chain running diagonally in a north-westerly direction from near the coast at Tanga. This chain, composed of the Eastern and Western Usambara and Pare Mountains, rises steeply to heights of from 4,000 to 7,000 feet. The climate is humid at the coast, becoming rapidly drier as one passes inland. The mountains exercise considerable influence on the local climate which is governed by the monsoon wind system, causing increased precipitation on the east slopes and marked rain shadows on the west. The climate and vegetation of this part of the region has been described by Moreau (1935).

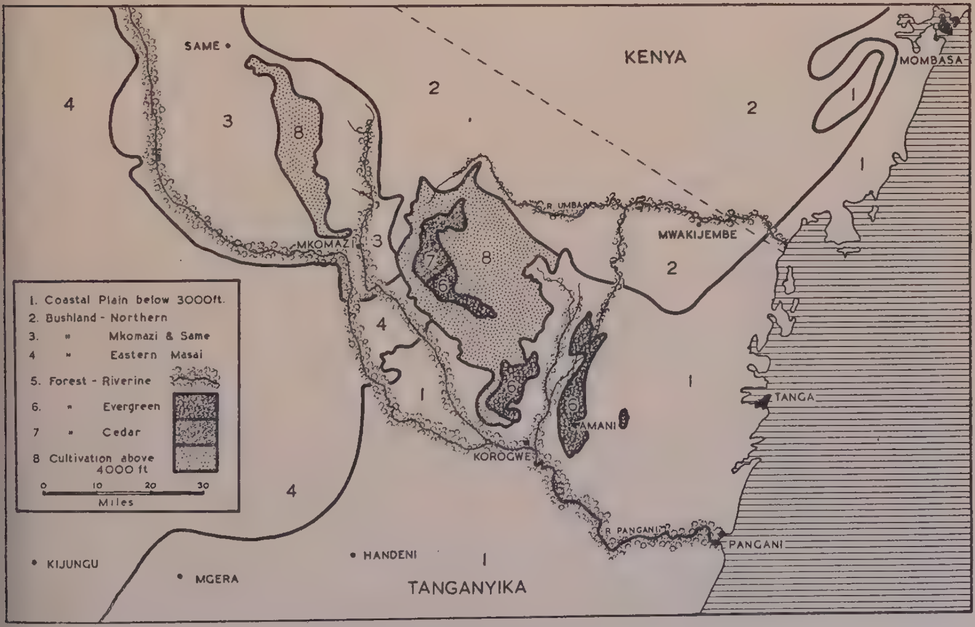

SAME
KENYA
MOMBASA
4
3
8
2
2
1
1
MKOMAZI
3
7
8
6
R. UMBA
MWAKIJEMBE
2
4
1
6
6
AMANI
1
TANGA
KOROGWE
R. PANGANI
PANGANI
4
KIJUNGU
MGERA
HANDENI
1
TANGANYIKA
1. Coastal Plain below 3000ft.
2. Bushland - Northern
3. " Mkomazi & Same
4 " Eastern Masai
5. Forest - Riverine
6. " Evergreen
7 " Cedar
8 Cultivation above 4000 ft
0 10 20 30
Miles

Fig. 1.—North-eastern Tanganyika, showing the eight zones discussed in relation to the distribution of termites.

Distribution in Relation to Vegetation Zones.

Eight zones. comprising different types of country have been selected as relating to the distribution of the termite fauna in north-eastern Tanganyika, as follows:

Plains.

1. Coastal plains below 3,000 feet.
2. Bushland north of the Usambara and Pare Mountains.
3. Bushland of the Mkomazi valley and Same district.
4. Bushland of the eastern Masailand plateau.
5. Riverine forest vegetation.

Mountains.

6. Tropical evergreen rain forest of Usambara Mountains.
7. Cedar forest of the Western Usambara Mountains.
8. Cultivated land over 4,000 feet.

The boundaries of these zones are shown in fig. 1. Use has been made of Gillman's vegetation map of Tanganyika (1949) where the limits of vegetation types are followed in these boundaries. Two termites, locally abundant and conspicuous, have been used to delimit the particular zones in which they occur; *Amitermes lonnbergianus* for the southern boundary of zones 2 and 3, and *Hodotermes mossambicus* for the eastern boundary of zones 3 and 4. The termites which have been recorded from each area are given in Table I.

TABLE I.

The distribution of termite species.

	Zone							
	1	2	3	4	5	6	7	8
KALOTERMITIDAE								
Kalotermes durbanensis Haviland	+	+	+					
K. kempae Wilkinson		+	+					
K. sp. (635)	+							
Neotermes sp. (401)		+						
N. sp. (457)	+							
N. sp. (135)	+							
Procryptotermes sp. (72)						+	+	
Cryptotermes havilandi (Sjöst.)	+	+	+		+	+		
HODOTERMITIDAE								
Hodotermes mossambicus (Hagen)			+	+				
RHINOTERMITIDAE								
Coptotermes amanii (Sjöst.)	+	+						
Schedorhinotermes lamanianus (Sjöst.)	+				+			
TERMITIDAE								
AMITERMITINAE								
Amitermes unidentatus (Wasmann)	+	+	+	+	+			
A. lonnbergianus (Sjöst.)		+	+					
A. sp. I	+	+	+	+				
A. sp. II	+	+	+					
Microcerotermes brachygnathus Silvestri	+	+						
M. edentatus Wasmann	+							
M. parvus (Hav.)	+	+	+	+	+			
M. masaiaticus Harris			+					
M. parvulus (Sjöst.)	+	+	+					
M. sp. I	+	+						
M. sp. II	+							

TABLE I—*continued.*

	Zone							
	1	2	3	4	5	6	7	8
TERMITIDAE (*continued*)								
AMITERMITINAE (*continued*)								
Anoplotermes sp. nr. *kilimandjaricus*	+					+		
A. sp. nr. *lateralis*	+	+				+		
A. spp.	+					+	+	+
TERMITINAE								
Crenitermes umbraticola Williams	+	+						
Euchilotermes sp.	+	+						
Cubitermes glebae (Sjöst.)	+	+		+			+	
C. umbratus Williams	+	+						
C. spp.			+					
Procubitermes goliathi Williams	+							
P. planifacies Williams	+	+						
Noditermes sp.	+	+		+	+			
Basidentitermes amicus Harris	+							
Angulitermes truncatus Sjöst.	+	+	+					
Promirotermes bellicosi (Wasmann)	+							
Pericapritermes dumicola Harris		+						
MACROTERMITINAE								
Pseudacanthotermes militaris (Sjöst.)	+							
Synacanthotermes zanzibarensis (Sjöst.)	+	+	+	+				
Allodontermes morogorensis Harris	+			+				
Macrotermes bellicosus (Smeath.)	+	+	+	+				
M. goliath (Sjöst.)	+							
Odontotermes amanicus Sjöst.	+			+	+	+		
O. amaniensis Sjöst.	+							
O. badius (Hav.)	+	+		+		+		+
O. boranicus (Ghidini)	+							
O. culturarum Sjöst.	+					+		
O. ? *kibarensis* (Fuller)	+							
O. latericius (Hav.)	+	+	+	+				
O. sp. nr. *patruus* (Sjöst.)	+		+					
O. rectanguloides Sjöst.	+						+	
O. stercorivorus (Sjöst.)	+							
O. tanganicus Sjöst.	+							
O. zambesiensis (Sjöst.)	+	+	+	+				
O. sp. I		+	+					
O. sp. II				+				
O. sp. III	+							
Ancistrotermes latinotus (Holmgren)	+	+						
Microtermes alluaudanus (Sjöst.)	+	+	+		+			
M. magnocellus (Sjöst.)						+		
M. redenianus (Sjöst.)	+	+	+	+				
M. luteus Harris		+	+					
M. vadschaggae (Sjöst.)	+	+	+	+				
M. spp.	+	+						
NASUTITERMITINAE								
Nasutitermes kempae Harris	+							
N. usambarensis (Sjöst.)	+				+	+		
Coarctotermes coarctatus (Sjöst.)	+	+	+					
Grallatotermes africanus Harris	+							
Trinervitermes rapulum (Sjöst.)	+							
T. segelli (Sjöst.)	+		+	+				
T. bettonianus (Sjöst.)	+							
T. spp.	+	+	+					

1. Coastal plains.

This zone is bounded on the west by the Shimba Hills and Eastern Usambara Mountains, and includes the Handeni district with the Ngu Hills. It is an area of comparatively high humidity. Along the coast, on a light sandy soil, there are coconut plantations, limited patches of grassland and thicket, and a small area of palm forest. Inland, where the country has not been altered by cultivation there is a drier type of thicket, changing to extensive *Brachystegia* woodland on the low hills (Pl. IV, fig. 1).

The coastal zone is considered first as the greatest variety of termites is found there. Sixty species have been recorded (see Table II), of which 20 species are restricted to this zone alone.

TABLE II.

The number of species represented in each family.

	All zones	Zone 1	2	3	4	5	6	7	8
KALOTERMITIDAE	8	5	4	3	0	1	2	1	0
HODOTERMITIDAE	1	0	0	1	1	0	0	0	0
RHINOTERMITIDAE	2	2	1	0	0	1	0	0	0
TERMITIDAE	61	53	31	22	16	6	8	3	2
AMITERMITINAE	*14*	*12*	*9*	*7*	*3*	*2*	*3*	*1*	*1*
TERMITINAE	*12*	*10*	*8*	*2*	*2*	*1*	*0*	*1*	*0*
MACROTERMITINAE	27	*23*	*12*	*10*	*10*	*2*	*4*	*1*	*1*
NASUTITERMITINAE	*8*	*8*	*2*	*3*	*1*	*1*	*1*	*0*	*0*
Total	72	60	36	26	17	8	10	4	2

One feature of this zone is the arboreal nests which are commonly found in the taller woodland. *Nasutitermes usambarensis* constructs nests of an earthy carton type; it is common throughout the coastal woodland extending up to the margin of the rain forest but is less frequent in the gallery forest along the rivers. *Schedorhinotermes lamanianus* has a similar distribution and occasionally builds subsidiary carton nests around dead wood on living trees with the main nest at the base, as described by Sjöstedt (1926). The nasute, *Grallatotermes africanus* (Pl. IV, fig. 2), is a species which builds large black carton nests generally associated with dense woodland of *Brachylaena hutchinsii* and other trees, found in small areas near the Eastern Usambara Mountains; it appears to be restricted to this area. *Microcerotermes edentatus* is also restricted to this coastal zone, and constructs carton-like nests on the larger tree trunks from 10 to 20 feet above ground; it is a rare species and has not been recorded from the drier country inland.

Two wood-living KALOTERMITIDAE are common, *Cryptotermes havilandi*, which is widespread throughout the whole region and *Kalotermes durbanensis*, which is restricted to the coastal plains. It is interesting that this latter species, unlike *K. kempae*, has not been found in branches of *Acacia* but occurs most commonly in *Brachystegia* and other trees. There is a single record of *Neotermes* sp. (No. 135) from soft-wood trees. *Coptotermes amanii* is also a common termite found in dry branches and stumps.

Amitermes unidentatus is common in drier thickets, it constructs small mounds of a woody carton material on stumps and fallen logs on the ground. Several termites belonging to the sub-families TERMITINAE and NASUTITERMITINAE construct earthy hummock-like mounds. A great variety of TERMITINAE is found in this zone, ten species being recorded. The most widespread small-mound builders are *Cubitermes* and *Noditermes*, the other genera are less common and often occur in separate galleries within the mounds of *Cubitermes*. *Promirotermes bellicosi* is occasionally found in mounds which it must have constructed, but it is not a common species and has not been found in the other zones. *Cubitermes umbratus* and *C. glebae* are generally found in woodland or associated with thicket clumps, while *C. glebae* alone occurs in short grassland. *Microcerotermes parvus* and *Amitermes unidentatus* are often found occupying part of the mounds built by *Cubitermes* spp. *Microcerotermes brachygnathus* also occurs in this habitat and nowhere else in the zone. Associated with grass tussocks in bushland and open country are mounds built by various species of *Trinervitermes*. These are grassland termites, locally abundant, and large numbers of their mounds are often aggregated. (Pl. V, fig. 1.)

Of the MACROTERMITINAE, *Pseudacanthotermes militaris* has a limited distribution. It has been found on the lower slopes of the Eastern Usambara Mountains and in the red-soil, *Brachystegia* woodland of the Ngu Hills. Where *Pseudacanthotermes* occurs it is generally very abundant, foraging in dry wood and building earth runways up thicket trees in a manner very similar to *Odontotermes*, which it appears to replace. *Synacanthotermes zanzibarensis* and *Ancistrotermes latinotus* are widespread species, both of which are found in a habitat similar to *Microtermes*, occurring in dry wood and plant litter on the surface. *Microtermes alluaudanus* and *M. vadschaggae* are abundant and widespread, while *M. redenianus* is a species more commonly associated with dry bushland.

Odontotermes is a genus represented in most parts of the country. The species *Odontotermes tanganicus* however is restricted to the coast, where foraging soldiers and workers have been commonly found in dead wood. In this zone *Odontotermes culturarum* and *O. rectanguloides* occur only on the lower hillsides. *Odontotermes* spp., like *Microtermes* spp., are very common in thicket and woodland, and they are also the most abundant termites found in cultivated land where the surface soil has been disturbed. Two large mound builders are found in this coastal zone; of these, *Macrotermes goliath* is common on the sandy soil near the coast and extends up to the margin of the rain forest. *Macrotermes bellicosus* is the more abundant species of the drier thicket inland, but it is generally distributed throughout the zone. (Pls. V, fig. 2 & VI, fig. 1.)

2. *Northern bushland.*

This zone lies to the north of the Usambara Mountains, at an altitude of 100 to 2,000 feet. It differs from zone 1 in being very much drier, with an annual rainfall under 30 inches. The vegetation is very uniform, mainly thicket of *Commiphora*, *Acacia*, *Grewia* and other trees on red earth, with seasonally swampy grassland on the low-lying grey soils and black clays. Although there does not appear to be such a variety of species as in zone 1, termite activity is just as great here. (Pl. VI, fig. 2.)

Amitermes lonnbergianus, a species with a limited distribution in East Africa, is very abundant in this zone. It occurs most commonly on grey soil among *Acacia* woodland on the margin of seasonally swampy ground, where it is the most abundant termite in dead wood and plant litter; it also occurs on red soils. The boundaries of zones 2 and 3 mark the southern limit of *A. lonnbergianus* in Tanganyika; the distribution of *Kalotermes kempae* and *Microtermes luteus* is exactly similar.

Kalotermes kempae is the most characteristic of the dry-wood termites; it has only been found in the dead branches on *Acacia* trees in the woodland belt commonly found around the margin of grassland swamps (Pl. VII, figs. 1 & 2). In this habitat it may be extremely abundant, some trees having every dead branch infested. Another species, *Kalotermes durbanensis* is more common on the higher ground and in a different species of *Acacia*.

A few species, typical of the coastal zone, extend into this bushland. For example, *Coptotermes amanii* is sometimes found in dry wood in shady thickets, and the soil-living *Anoplotermes* is also found in shade. *Amitermes unidentatus* is widespread in this zone, and two additional species of *Amitermes* occur which are not common but are characteristic of dry bushland.

Termites of the sub-family TERMITINAE are not generally common, but mounds of *Cubitermes* may be locally abundant, restricted to the shade of thicket and woodland. A number of mounds in *Grewia* thickets on red sandy soil were examined; *Cubitermes umbratus*, and *Cubitermes glebae* were found to be equally common, while *Euchilotermes* sp. and *Crenetermes* sp. were less frequent. In this zone *Noditermes* is generally associated with mounds of the larger *Cubitermes*. *Pericapritermes dumicola* is rare and has only been recorded from one stony hillside at Mwakijembe, where it constructs mounds superficially very similar to those of *Cubitermes*.

Of the MACROTERMITINAE, *Macrotermes bellicosus* is the common builder of large mounds on red soils. The *Microtermes* are of interest; *Microtermes alluaudanus* is abundant but *M. vadschaggae* is very rare, in contrast to the thicket of Masailand (zone 4). *Microtermes redenianus* and *Microtermes luteus* are commonly found foraging in dead wood. Two species of *Odontotermes*, *O. latericius* and *O. zambesiensis*, are very abundant in dead wood, and their earth-runs on *Commiphora* and other trees are a conspicuous feature of this bushland.

A *Trinervitermes* sp. is locally common on almost bare ground between thicket clumps, where it makes large hummock-like mounds, but the grassland *Cubitermes* and other *Trinervitermes* are absent. No termites are found on the seasonally swampy clay.

3. *Bushland of the Mkomazi valley.*

This zone has an even lower rainfall than zone 2. It includes the Mkomazi valley, which lies within the rain shadow from the Usambara Mountains, and the bushland extending to the Pangani (Ruvu) river. (Pl. VIII, fig. 1.)

Hodotermes mossambicus is the most conspicuous termite in this zone. The small conical refuse dumps are seen on most open ground and hard-pans. The eastern limit of *Hodotermes* is well defined and is shown by the eastern boundaries of zones 3 and 4 on the map.

This dry bushland resembles that of zone 2 and the same species of *Kalotermes*, *Microcerotermes* and *Amitermes* occur, but the thickets are more open and offer little shade, so the common *Cubitermes* are absent. Other members of the TERMITINAE are not recorded, with the exception of *Angulitermes truncatus* which frequently occurs in dry twigs and dikdik dung.

The same species of MACROTERMITINAE are found as in zone 2, but here *Microtermes alluaudanus* and *M. vadschaggae* are equally abundant and other species of *Microtermes* are rare.

4. *Bushland of the Masai plateau.*

This zone forms the eastern margin of the Masailand plateau and consists of dry bushland and dense thicket. *Hodotermes mossambicus* is common on hard open ground but *Amitermes lonnbergianus* is absent.

No representatives of the KALOTERMITIDAE were found here, though it is thought unlikely that they should be absent from a zone with so many woody shrubs and trees, including *Acacia* spp. *Microcerotermes parvus* was the common termite of dry branches and snags as well as in fallen logs on the ground.

Amitermes unidentatus and the TERMITINAE were locally abundant where the very dense thicket provided shade. *Cubitermes glebae* was common, but here the nests were mainly below the surface without the conspicuous mounds observed in zones 1 and 2. *Noditermes* was found occasionally.

The dry thicket on red soil offers similar conditions for the MACROTERMITINAE as in other zones. *Odontotermes latericius* and *O. zambesiensis* are still the most abundant species and the large mounds of *Macrotermes bellicosus* occur on sloping ground and swamp margins. *Microtermes vadschaggae* is more abundant than *M. redenianus*, but other species of *Microtermes* were not recorded.

5. *Riverine forest.*

Throughout the plains in north-eastern Tanganyika a uniform type of vegetation is found along the larger rivers, tall forest, with little undergrowth, providing deep shade in contrast to the surrounding bushland. *Schedorhinotermes lamanianus* is found in all this forest even in the desert-like Mkomazi valley. *Nasutitermes usambarensis* which is common on the forest margin of the Usambara Mountains extends into the gallery forest along the Umba river. (Pl. VIII, fig. 2.)

Microcerotermes parvus, *Microtermes alluaudanus* and *Odontotermes badius* are frequently found in the plant litter of the forest floor. These species may be found foraging here at all times of the day, in contrast to the open bushland where they are rarely seen between 11 a.m. and 5 p.m., except during the rains.

6. *Rain forest.*

The remaining zones have a more specialised vegetation. The rain forest of the Usambara Mountains is unlike any other vegetation type in the country and termites are very rarely found within it. It occurs on the east slope of the Western Usambara where the rainfall is high, and over most of the Eastern Usambara Mountains where the boundary of this zone follows the 3,000 ft. contour. It is tall forest with trees from 60 to 80 feet in height and little undergrowth (Pl. IX, fig. 1), but there is a deep leaf litter on the forest floor which remains damp and is often covered in mould. A small part of this zone is under cultivation and there is some natural grassland on the summit of the hills.

Some of the common termites extend into the forest at its lower margin but only *Procryptotermes angulatus* and *Anoplotermes* spp. have been recorded within the forest proper. *Procryptotermes* is probably very common, although rarely seen, as it occurs in the uppermost canopy. It has usually been found in the top branches of recently felled forest trees, inhabiting the dead snags and branches, a typical Kalotermitid habitat.

Grassland country occurs on the hill tops of the Eastern Usambara Mountains at an altitude of about 4,000 ft. *Odontotermes amanicus* was found here but, except for the forest *Anoplotermes*, no other termites were recorded. A small area which had been recently cleared of forest and cultivated was examined and only *Anoplotermes* found within the soil, in contrast to the Amani plantations which have been cultivated for 50 years, where *Microtermes vadschaggae* and *Odontotermes amanicus* were common. *Odontotermes* is otherwise rare in this zone and only recorded from roadside and river bank where the forest is more open. *Odontotermes culturarum* and *Microtermes magnocellus* are species characteristic of the lower mountain side. *Nasutitermes usambarensis* constructs its arboreal nests on the tall trees at the forest margin but it has never been recorded from within the forest where the light intensity is low.

7. *Cedar forest.*

The dry cedar forests (*Juniperus procera*) of the Western Usambara Mountains also have a very small termite fauna. *Procryptotermes angulatus* was found in soft-wood trees in the forest and *Odontotermes rectanguloides* occurred occasionally foraging in dead wood. Some trenches were dug in this zone but no termites were found in the soil (see Table III). In the valleys, however, there are glades of short grassland and *Odontotermes rectanguloides* was common here. Large mounds aggregated on the margin of swampy areas are probably built by this species (Pl. IX, fig. 2). *Anoplotermes* sp. and *Cubitermes glebae* are locally very abundant also; they construct small hummock-like mounds of grey soil often among the roots of small herbs (Pl. X, fig. 1). No other species was found.

8. *Cultivation over 4,000 ft.*

Much of the country in the Western Usambara Mountains has been cleared of forest and intensively cultivated for a very long time. Here *Odontotermes badius* is common in dead wood and builds low mounds. *Cubitermes umbratus* was found in a large aggregation of mounds on a heavily grazed and eroded hillside (Pl. X, fig. 2), only a small proportion of the mounds being inhabited. Also a single species of *Anoplotermes* was recorded differing from that found in the forest glades.

This cultivated land lies between 4,000 and 6,000 ft. and *Microtermes* was not found at that altitude. But at 4,000 ft. and below, *Microtermes vadschaggae* was common in the native cultivation on the steep hillsides. Descending the mountains the first termites typical of the plains were found at about 3,800 ft., *Microcerotermes parvus* occurring higher than *Amitermes*, *Odontotermes* or *Trinervitermes*. (This distribution is illustrated diagrammatically in fig. 2.) Collections were made at only two places on the Pare Mountains and on both the east and west slopes the termites typical of the plains were found in the dry hillside thicket, up to an altitude of 4,500 feet.

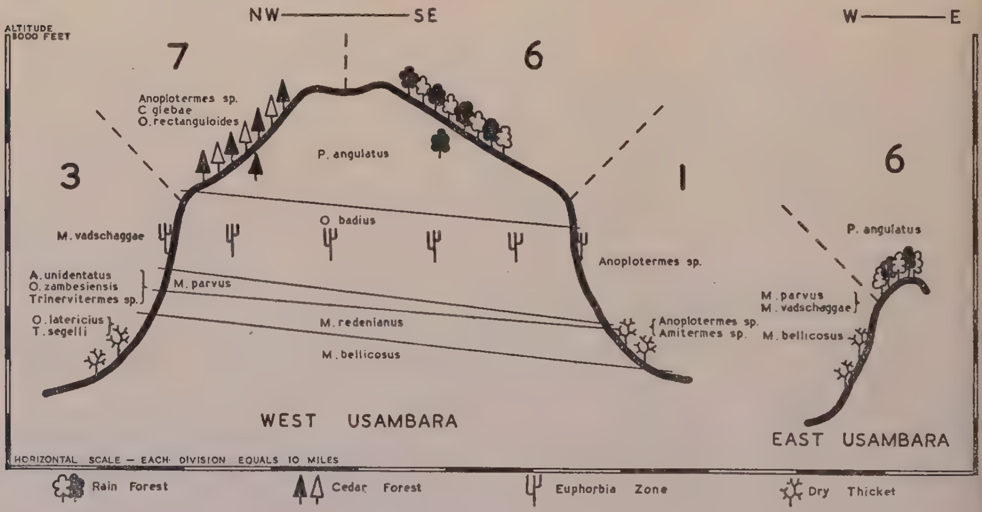

NW — SE
W — E
ALTITUDE 8000 FEET
7
6
3
1
6
Anoplotermes sp.
C glebae
O. rectanguloides
P. angulatus
O badius
M. vadschaggae
Anoplotermes sp.
A. unidentatus
O. zambesiensis
Trinervitermes sp.
M. parvus
O. latericius
T. segelli
M. redenianus
M. bellicosus
Anoplotermes sp.
Amitermes sp.
P. angulatus
M. parvus
M. vadschaggae
M. bellicosus
WEST USAMBARA
EAST USAMBARA
HORIZONTAL SCALE — EACH DIVISION EQUALS 10 MILES
Rain Forest
Cedar Forest
Euphorbia Zone
Dry Thicket

Fig. 2.—A diagram of the Usambara Mountains to show the distribution of termites in relation to altitude and their upper limit on the hillside.

The Collection of Soil-dwelling Termites.

Two methods were used for the collection of the less conspicuous subterranean termites, in order to obtain some information on their relative abundance.

The first method was to dig a number of trenches of uniform size in a variety of soil and vegetation types. These were dug to a depth of 1 metre, 5 metres long and 1 metre wide in sites free from obstacles such as trees and rocks, selected at random. The depth at which the larger insects were found in the soil was recorded. For comparison between the rain forest (zone 6) and woodland near the lower forest margin (zone 1), ten of these trenches were dug in deep red soil. In rain forest, *Anoplotermes* was recorded from only four trenches, but, in the equivalent area under woodland, termites occurred in all the trenches and a total of 12 species was recorded. In addition, five trenches were dug at Amani, in land which had been cleared of forest for 50 years; *Microtermes vadschaggae* was found to be common here and occurred in all the trenches whilst *Microtermes* sp., *Odontotermes stercorivorus* and *Anoplotermes* sp. were also found. In similar country, which had only been cleared of forest for 20 years, the forest-dwelling *Anoplotermes* sp. was the only termite recorded. These results are given in Table III.

TABLE III.

Collections made from trenches.

Zone	Locality	No. of trenches	Vegetation	No. of species	No. of records	Most frequent species
2	Mwakijembe	10	thicket	13	41	*Microtermes redenianus*
1	Handeni	5	woodland	8	26	*Anoplotermes* sp. *Microtermes alluaudanus*
1	Kizugu, nr. Amani	10	woodland	12	67	*Pseudacanthotermes militaris* *Microtermes alluaudanus*
6	Amani	5	cultivation	4	26	*Microtermes vadschaggae*
6	Amani	10	rain forest	2	5	*Anoplotermes* spp.
6	Amani	2	mountain grassland	1	2	*Anoplotermes* sp.
7	Shume	5	cedar forest	0	0	

Similar trenches were dug in dry bushland at Mwakijembe (zone 2). Termites were recorded from the total of 12 trenches dug on red and red-brown soils and 17 species were represented. No insects were found in a trench dug on the seasonally swampy black clay. In thicket at Handeni (zone 1) termites were found in all the six trenches dug on red sandy soil and 10 species were recorded. Although a greater variety of termites was reported from zone 1, these results suggest that a larger proportion of the termites living in hot and dry bushland are subterranean forms.

The second method of estimating the termite population was by exposing a number of wooden pegs to termite attack. These were cut from trees of *Commiphora schimperi*, 50 cm. in length and roughly 4 cm. in diameter; they were driven into the ground to a depth of 30 cm., arranged in blocks of 20 pegs. These were examined after about three months and the number of pegs which had been attacked by termites was recorded. The average number of pegs attacked, expressed as a percentage, is shown for each zone in Table IV.

These results confirm field observations and data from the trenches. In contrast to forests elsewhere, termites are rare in the rain forest of the Usambara Mountains, although they are capable of invading that country once the forest has been cleared. It is also shown that the termites foraging in dead wood in the dry bushland of the plains are almost equally abundant in zones 1 and 2. The greater number of species recorded from the coastal area are mainly humus-feeding TERMITINAE, while subterranean termites are very much more frequent in dry bushland.

TABLE IV.

Commiphora pegs attacked by termites.

Zone	No. of pegs exposed	Locality	Vegetation	Per cent. attacked
1	120	Handeni	woodland	70
2	280	Mwakijembe	thicket	56
6	80	Amani	cultivation	37
6	120	Amani	rain forest	0

General Observations on Distribution.

From the foregoing account it would appear that the distribution of termites shows a definite interrelation with topography, climate and vegetation in north-eastern Tanganyika. The more humid woodland near the coast shows a greater variety of humus-feeding TERMITINAE and the number of species recorded is almost twice as great as in the other zones of comparable size. There is also a greater variety in the habitats where these species are found. Some are arboreal forms, others inhabitants of dry branches, fallen logs and plant litter, whilst others again are subterranean and grassland species. Such variety is not found in the dry thickets inland. The number of termites may be as great but the species are fewer. In dry bushland the most prevalent termites are the subterranean species, foraging dry woody material on the surface. The occurrence of surface-nesting species is restricted to clumps of thicket where low bushes offer shade. Species that nest in trees cannot survive in open woodland, and this is illustrated by the frequency with which they are found in the gallery forest along the rivers.

The forests are most notable for the few termites which occur within them. Emerson (1928) records over 100 species from the forests of the Belgian Congo, but in the Usambara Mountains only two species can be regarded as inhabitants of the rain forest.

It is suggested that climate is the principal factor determining the distribution of termites in this region. The nature of the soil does not have such a great influence except where the land may become seasonally inundated.

Biological Notes on the Termites occurring in the Region.

The species are listed below in systematic order, their distribution throughout the region having been given in Table I. The classification follows that of Snyder (1949).

KALOTERMITIDAE.

Kalotermes durbanensis Haviland.

The proportion of soldiers in a colony varies greatly. Alates have been recorded in both April and September from the same locality, and nymphs are present over a long period.

This species is locally common throughout zone 1, in dead snags and dry branches on living trees, but is not recorded from *Acacia* spp. In zones 2 and 3 it is found most commonly in a different species of *Acacia* which occurs on higher ground. The colony is generally present in dead wood immediately adjacent to the living tissue.

The alate nymphs collected in the last instar in July were reared in culture tubes and the mature alates emerged in November and January. Other cultures were set up in July without these alate nymphs; these produced alate nymphs between January and April, and mature winged forms were found in the colonies in April also. A few colonies without mature soldiers produced soldier nymphs during this period.

Kalotermes kempae Wilkinson.

Soldiers are fairly numerous compared with the workers. Alates have been found in June, and, together with alate nymphs, in October. The queen is not distended, and both reproductive forms are able to move freely within the galleries, which are elongate inter-communicating tunnels with clean surfaces in the dry wood.

This species occupies dead branches and snags, similar in appearance to the habitat of *K. durbanensis* but in contrast it has only been recorded from *Acacia* trees. It is especially common where these trees form pure stands on the margin of swampy ground, often occupying all available dry branches (see Pl. VII, figs. 1 & 2). It is rarely found in dead wood on the ground, probably because, when the branches fall, the colonies are at once exterminated by ants.

Attempts were made to rear the nymphs in culture tubes, but these did not survive more than a month.

Neotermes sp. (No. 135).

Soldiers are numerous; alates and alate nymphs were collected in February from the single colony recorded. These termites were confined to a hard dry branch of an aromatic timber, probably *Diplorhynchus* sp., found in woodland at Handeni.

Procryptotermes sp. (No. 72).

Soldiers are not very numerous in proportion to the nymphs. Alate nymphs were found in June and July, and again, together with mature alates, in November and December. Reproductive forms have also been collected from the galleries.

Elongate tunnels are excavated in dry branches and resemble those of the other Kalotermitidae. It is probable that this species is very common in dead branches of rain-forest trees from 60 to 80 ft. above ground, since it was always found on examining trees which had been recently felled. In the drier cedar forests, this species was recorded from dead wood among roots at ground level.

Some nymphs of this species were reared in culture tubes and plates. It was of interest that alates were produced with great regularity within these artificial nests when kept in a darkened cupboard. For example, a colony set up in October produced alate nymphs by the following July and mature alates in November. Other colonies of nymphs collected in November and also in March gave the same result; alate nymphs were present by July and the alates in November. It was also noticed that colonies set up without soldiers produced soldier nymphs within 3 to 4 months; these did not occur in colonies where soldiers were present among the original nymphs.

Cryptotermes havilandi (Sjöstedt).

Soldiers are few in proportion to the workers. Alate nymphs have been found in June and alates recorded from the same area in October. In another locality mature alates were found in May. *Cryptotermes* has smaller colonies than other species of KALOTERMITIDAE and it is never very abundant in one area. It has been found in dry branches of several species of soft-wood trees.

Cultures of this species kept in the laboratory did not thrive. Nymphs collected in October produced alate nymphs the following April, but these did not survive.

HODOTERMITIDAE.

Hodotermes mossambicus (Hagen).

Only major and minor soldiers and workers have been collected. The nest, which is subterranean and apparently very deep, has not been located. The species is characteristic of hard-pan soils in the driest part of the region. The eastern limit of its distribution follows the boundaries of zones 3 and 4 on the map.

RHINOTERMITIDAE.

Coptotermes amanii (Sjöstedt).

Soldiers are numerous among the foraging workers. Alate nymphs have been found in March and the mature alates have been caught in flight in November. These alates emerged at 6.30 p.m. from the lintel of a door and cracks in the stone wall. The exit from the nest was surrounded by soldiers which discharged a white fluid when aggravated. After about half an hour the alates alighted but few paired, most of them running into cracks in the wall still retaining their wings. Flight was also observed on the same date the following year, although the distribution of rain during the preceding days was very different.

Coptotermes has been commonly found in the woodwork of buildings, but also it is locally very abundant in thicket and woodland. The galleries are distinct from those of the KALOTERMITIDAE, being partly lined with frass-like material. The main nest is subterranean but has not been located, even on extensive excavation under infested stumps.

Schedorhinotermes lamanianus (Sjöstedt).

Major and minor soldiers occur, the minor soldiers being the more abundant. Young alate nymphs were found in November and in the last nymphal stage in December. Mature alates were caught in flight in the same area at 3 a.m. on a damp foggy night in March. They were recognisable by the powerful acrid smell which is also emitted by the soldiers when irritated. Like *Coptotermes*, the flight lasted about half an hour and no pairing was observed. The termites swarmed over the walls of the house and gradually made their way upwards, disappearing into cracks near the ceiling.

Nests are constructed of pulpy material generally in crevices and buttress roots of large trees. Covered runways lead from this to dry branches and occasionally to subsidiary nests above. The king and queen are found in undifferentiated galleries in the basal nest. Termitophilous larvae of the Tineid moth, *Plastopolypus* (*Passalactis*) *tentatrix* (Meyr.), are found with this species and no colony has been recorded without them.

TERMITIDAE.

AMITERMITINAE.

Amitermes unidentatus (Wasmann).

Soldiers are abundant among the workers. Young alate nymphs were recorded in September and alate nymphs in the last stage in June. Mature alates have been found in the nest in March, June and October, which suggests that the production of alates is not confined to any special season.

The nest is generally a mound of dark woody material constructed over fallen logs and stumps, or sometimes grey soil mounds having the galleries lined with this woody substance. The reproductive forms have only been found rarely within the mounds, living at ground level in undifferentiated galleries; in several nests they were not located even after extensive excavation.

This is a particularly common and widespread species on well drained soils, generally among thicket and scrub land and foraging in woody plant litter.

Amitermes lonnbergianus (Sjöstedt).

Soldiers and foraging workers are locally common and a few alate nymphs were observed in October. Only a single nest has been recorded; this was a small hummock with the queen at ground level, constructed at the margin of woodland.

This species is easily recognised and it was therefore possible to obtain a fairly accurate idea of its distribution within the region. The southern limit is shown in the map forming the southern boundary of zones 2 and 3. *A. lonnbergianus*, in some parts, may be the most abundant termite in dead wood; together with *Kalotermes kempae* and *Microcerotermes* sp. it is especially common in the *Acacia* woodland on the margin of grassland in zone 2 (Pl. VII, fig. 1), occurring in earthy tunnels in fallen branches.

Amitermes sp. I.

This species constructs small hard mounds, most frequently in dry bushland, but also in damp situations such as the margin of swamps. Alate nymphs were found in February, and alates were present in the nest in October. Soldiers and workers are found in dead wood, and in separate galleries within the mounds of other termites, such as *Cubitermes*, *Trinervitermes* and *Odontotermes*.

Amitermes sp. II.

A small species only occasionally collected from mounds on grey soils, or foraging in dead wood in dry bushland. Alate nymphs in the last instar were found in May and June.

Microcerotermes brachygnathus Silvestri.

Soldiers are few in proportion to the workers. Alate nymphs were found in February and November, and mature alates were collected in June and November. Soldier nymphs were also found in the nest at this time.

The nest is a small mound with the queen easily found at ground level, but this species also occurs in mounds built by *Amitermes* and *Cubitermes* where it is restricted to distinct galleries, lined with a woody layer. It is infrequent in more open country.

Microcerotermes edentatus Wasmann.

Soldiers and workers with numerous nymphs have been found in arboreal nests. Mature alates and alate nymphs were collected with these in December.

Nests are of a carton material adpressed to tree trunks. No queen was found in this upper nest and it is possible that the main nest is subterranean. Soldiers and workers have been collected from dry wood but it is an uncommon species limited to the damper woodland of the coastal zone.

Microcerotermes parvus (Haviland).

Workers collected while foraging are very much more abundant than the soldiers. Alate nymphs have been found in the last instar in March, October and November, and mature alates in the nest in April and May and also from

October to December. These would be ready for flight in the two rainy seasons in this country.

M. parvus is one of the most widespread species found in the region; it occurs in all the vegetation types of the plains and extends further up the mountain side than any other lowland species. It is generally found in dry stumps and branches, and invades the habitat typical of the Kalotermitidae where these are not abundant. The nest is of a hard carton type often constructed within mounds built by *Cubitermes* and *Trinervitermes*.

Microcerotermes masaiaticus Harris.

Only soldiers and workers have been recorded, these were found in dead wood in dry bushland in the Same district.

Microcerotermes parvulus (Sjöstedt).

This species is widespread throughout the coastal plain and the adjacent woodlands. The nests are of carton and usually below the surface in cultivated or sandy soils, but forming small mounds in seasonally swampy grassland. Dead branches on living trees are often invaded. Mature alates were found in galleries in dead wood in June.

Microcerotermes sp. I.

Soldiers and foraging workers have been found in logs and dry branches in bushland, and, in one area in dry cow-dung. Only one queen was found.

Anoplotermes spp.

The habits of the different species of *Anoplotermes* appear to be very similar. Alate nymphs of *Anoplotermes* sp. (near *lateralis*) were observed in July and mature alates were collected from the same locality in September; alates were also found in March, in drier woodland. Alate nymphs of *Anoplotermes* sp. (near *kilimandjaricus*) were found in dry bushland in March, and of a third *Anoplotermes* in April. Worker nymphs were occasionally recorded but the nests are very diffuse.

A nest of an *Anoplotermes* sp. was found in woodland at the foot of a tree. The mound was scarcely perceptible in the soft damp soil and small tunnels penetrated among the roots to a depth of 2 or 3 in. in the superficial humus. The queen was in an undifferentiated tunnel together with a few lethargic worker termites. A very similar nest of another species was found under an overhanging rock.

Anoplotermes sp. (No. 311) was found under different conditions to the other species. It constructs hard mounds of grey soil, about 6 in. high, with the queen at ground level, very similar to those of *Cubitermes*. These were found in the short-grass glades in the cedar forest of the Western Usambara Mountains.

TERMITINAE.

Crenetermes umbraticola Williams.

Soldiers and workers have been collected in small colonies. Alate nymphs were found in the last instar in June and October, while mature alates occurred in a nest in April. This species has been found living in the same mounds as *Cubitermes umbratus*. It is not possible to distinguish separate galleries as the workers of the two genera are very alike. In one mound the two queens were only about 3 in. apart, just below ground level. It is rarely found in unoccupied *Cubitermes* mounds. Probably this species is more abundant than appears in the records as it is superficially very like *Cubitermes* and difficult to recognise in the field.

Euchilotermes sp.

Reproductive forms, soldiers and workers have been collected and alate nymphs were found in June. This species constructs small grey soil mounds resembling those of *Cubitermes* but it has not been found with another species. In a sample of 20 mounds examined in *Grewia* thickets at Mwakijembe (zone 2), *Euchilotermes* was found in two and *Crenetermes* in one mound. The colonies are very small and generally only one or two soldiers are present.

Cubitermes glebae (Sjöstedt).

This species is widely distributed in the less dry regions of the region under consideration. Mounds are small, varying in height from a few inches to one foot, the proportion of the nest below ground varying inversely. In thicket or woodland the mounds are scattered, unlike those of *C. umbratus*. Aggregations of mounds are common on grey soil near the margins of seasonally swampy grassland, on the plains, and again in the short-grass glades in the cedar forests at an altitude of 6,000 feet in the Western Usambara Mountains. In the latter habitat, the mounds resemble those of *Anoplotermes*, also locally abundant (Pl. X, fig. 1). Mounds on the plains grassland are shared on occasion with *Microcerotermes parvus* and *Amitermes* sp.

Mature alates have been found in the nest in January, February, April, June and November according to locality. Alate nymphs have been found at most times of the year and it is suggested that alates remain for long periods in the mounds, awaiting suitable weather conditions for emergence.

The proportion of soldiers to workers in the colony appears to be greater at higher elevations than on the plains.

Cubitermes umbratus Williams.

C. umbratus is common throughout the *Brachystegia* woodland and dry-bush of zones 1 and 2. Mounds are small earthy structures about one foot in height, frequently occurring in partial shade (Pl. X, fig. 2). Where there are many mounds aggregated in one area, it is usual to find a large proportion no longer occupied.

The grey soil of a typical mound constructed partially under a log was analysed by Mr. P. R. Hesse and compared with the surface soil surrounding it. From the Table below it will be seen that:—

(i) the moisture content is twice as great within the mound.

(ii) the proportion of clay in the mound is much higher than in the surrounding soil and there is very much less sand. Consequently the mound has a greater water-holding capacity and this fact was confirmed by analysis. There is also a greater pore space in the mound.

(iii) the mound proved to be more alkaline than the surrounding soil.

(iv) the quantities of phosphate, nitrogen and water-soluble salts were all considerably greater within the mound.

Analyses of mound of *Cubitermes umbratus*.

Mechanical Analysis (%).

	Moisture	Organic matter	Sand	Clay
Mound soil ..	4·9	2·9	26·5	67·2
Surrounding soil ..	2·5	2·3	63·0	30·8

Chemical Analysis.

	Phosphates p.p.m.			Nitrogen (%)	pH	Total water-soluble salts (%)
	Adsorbed	Acid soluble	Ads. + acid			
Mound soil ..	85	20	220	0·23	6·2	0·16
Surrounding soil ..	25	0	50	0·11	5·6	0·03

Procubitermes goliathi Williams.

A single record of soldiers, workers and alate nymphs from the wall of a mound of *Macrotermes goliath* in *Acacia* grassland at Ngomeni.

Procubitermes planifacies Williams.

Two records, each of a few soldiers and workers found in the soil at Ngomeni and Mwakijembe.

Noditermes sp.

The nest of this species is a small grey mound of fine earth, fairly commonly seen in the damper woodland of the eastern hill slopes.

A mound of this type was found adpressed against the decaying wood of a large tree (*Albizzia* sp.); it was brought into the laboratory and opened. The alates were occupying the uppermost galleries, flying out in large numbers as soon as the mound was broken (3 p.m.). These congregated by the window, while others, incarcerated before flight, remained quivering and restless. Those aggregated by the window climbed the wall and stood motionless in the sun with head uppermost and the abdomen raised while others continued wandering. The wings were shed just before or sometimes after pairing, either sex first, but no wings were shed without flight. This was also observed by Luscher (1951). Some artificial nests containing damp sand were left on the table; after shedding their wings the pairs ran rapidly down the wall away from the light and readily entered these nests where they at once commenced to excavate the first royal cell in the damp sand. The colonies established in this way survived for the next four months, and the following observations were made:

3.x.50		Flight lasting half an hour, cell excavated in damp sand
6.x.50	3rd day	Copulation?
1.xii.50	28th day	First eggs observed
10.xii.50	37th day	About 26 eggs in one nest
1.i.51	59th day	First nymphs observed
4.ii.51	94th day	Worker nymphs observed
10.ii.51	100th day	First soldier nymph observed
25.ii.51	115th day	The colony died off, containing 2 adult soldiers and 2 adult workers.

Basidentitermes amicus Harris.

Soldiers are fairly frequent among the workers and alates have been collected in flight in November.

The nest of this species is subterranean and was not located, although extensive excavations were made around the small earth tunnels from which the alates were seen emerging. It is not always found associated with other species of termites although one colony was recorded from a nest of *Synacanthotermes zanzibarensis*. It is uncommon and most frequently found in fallen branches and the superficial humus layers of the soil, in a habitat very like that of *Anoplotermes* sp.

A flight of these termites was observed in November, at 4 p.m. after a day of heavy rain. The alates were fluttering weakly and not travelling any great distance from the parent nest. Some paired and shed their wings within five yards of the nest entrance. The pairs adhere very strongly and cannot be persuaded to separate. Some of these were brought into the laboratory and introduced into artificial nests; the first cells had been constructed within the damp sand in under three hours. The first eggs were observed in these colonies after 20 days and the number of eggs increased steadily for the next month. After 45 days the first nymphs were observed. The colonies did not develop further.

Angulitermes truncatus Sjöstedt.

A few soldiers and workers were collected in very dry bushland where this species may be locally fairly frequent. These were foraging in plant litter, twigs and dry patches of dikdik dung.

Soldiers, workers and mature alates were collected from two separate localities in February (Ngomeni and Handeni). One flight was observed in woodland at 6.30 p.m., on a damp cloudy evening, after there had been a heavy shower of rain in the afternoon. Alates were seen emerging, near a path, from a small hole which was surrounded by soldiers and workers. No nest was located but only diffuse tunnels in the soil.

Promirotermes bellicosi (Wasmann).

Soldiers and workers have been found with young alate nymphs in February and nymphs in the last instar in June. The mature alates were found in the nest in November.

The nest is a cylindrical mound of the *Cubitermes* type but occasionally the colony occupies part of a mound constructed by another species. *Microtermes* sp., with fungus gardens, has been found in the uppermost regions of these mounds. *P. bellicosi* is fairly frequent in the coastal woodland (zone 1).

Pericapritermes dumicola Harris.

Nests of this species have been found in a single locality at Mwakijembe. The alate nymphs were found in the last instar in June. *P. dumicola* constructs small mounds among the roots of thicket trees on a stony hillside. Several such colonies were found in a limited area and a few soldiers and workers occurred in isolated tunnels in the soil.

MACROTERMITINAE.

Pseudacanthotermes militaris (Sjöstedt).

The minor soldiers are abundant among the foraging workers found in dead wood, but the major soldiers are less common. For example, a number of these termites was observed constructing an earth tunnel up the stem of a small tree, the black minor soldiers being arranged around the mouth of the tunnel in a single line, while the workers were building immediately behind them. The larger red soldiers were only found near the base of the run and did not appear to be concerned with the defence of the builders.

Fungus gardens were found in one nest constructed in the wall of a mound of *Macrotermes goliath*; these were castellated in form.

Synacanthotermes zanzibarensis (Sjöstedt).

A nest was found among the roots of a palm (*Hyphaene* sp.). The mound was not conspicuous and fungus gardens were found about six inches below the surface. These were flattened and plate-like, about 4 to 6 in. in diameter and scattered throughout the nest. The queen was slightly to one side in a chamber of hardened earth and the greatest activity was around this royal cell.

Soldiers and workers are common throughout the plains. They are found in dry wood and constructing earth tunnels up thicket trees.

Allodontermes morogorensis Harris.

Soldiers and workers have been found in dead wood throughout the southern part of this region, and they construct earth runs on the smaller trees in thicket.

Macrotermes bellicosus (Smeathman).

Both major and minor soldiers are very variable in size. They have been collected with foraging workers in dead wood, where they are active mainly in the early part of the day. This species constructs the large mounds which are often a conspicuous feature of bushland; it was not found at elevations over 4,000 ft. and never in forest. The mounds are up to 10 ft. high and are often covered with thicket. They are generally built on the red and red-brown soils of slightly sloping ground.

The last stages of a flight of this species was observed in Amani, in December, at 8 a.m. There had been heavy showers the previous day but no rain overnight. A column about 20 yards long, comprising soldiers and workers of all sizes was proceeding along the roadside and entering the nest by small holes five yards away from the mound itself. The ground was scattered with wings which had been shed but the de-alated pairs were not found, except where they had been attacked by the large ants foraging in the vicinity. After a similar flight at Mwakijembe the de-alated pairs were found constructing a cell in the top layer of the soil.

Macrotermes goliath (Sjöstedt).

This species constructs large earth mounds which are indistinguishable externally from those of *M. bellicosus*. It is not so widely distributed in this region. Alate nymphs were found in the last instar in November.

Odontotermes amanicus Sjöstedt.

A common species of hillside thicket, frequently foraging in dead wood. It has been found in a great variety of vegetation types from the margin of the Usambara rain forest to the dry thicket of Masailand. Alates were collected in a nest during October.

Odontotermes amaniensis Sjöstedt.

A single record from a small mound in cultivated land (Magrotto, near Amani).

Odontotermes badius (Haviland).

This is a widespread species commonly foraging in dead wood in all vegetation types up to the forest margin. The nest is generally a low mound with open shafts (Pl. V, fig. 2) on well drained soils. Alates have been observed emerging from the nest at 7 p.m. in September and in December and January.

In September, alates were attracted to a light in the house. The main swarm lasted only about half an hour but individual alates were noted between 6 and 8 p.m. Wings were shed and pairing took place immediately. These pairs were collected and introduced to damp sand in which they commenced to build at once. A few pairs put into dry sand made no attempt to build whilst those on medium and fine sand appeared to build more successfully than those on coarse sand. These colonies were left undisturbed but those building against the glass wall of the container could be observed:

9.ix.51		Flight and first cell constructed
29.ix.51	20th day	First eggs observed
14.xi.51	46th day	Increase in number of eggs
10.xii.51	71st day	First nymphs observed in nests with greatest number of eggs
17.i.52	109th day	Increase in number and size of nymphs
4.ii.52	127th day	The first adult soldier observed
9.ix.52	366th day	One pair surviving with no surviving nymphs.

Odontotermes boranicus (Ghidini).

A single record of soldiers and workers from elephant dung in dry thicket at Mwakijembe.

Odontotermes culturarum Sjöstedt.

Soldiers and foraging workers have been found in dead wood on the eastern hillsides of the Usambara and Pare Mountains.

Odontotermes ? kibarensis (Fuller).

A single record from dry leaves among a thicket in hillside woodland (Mgera, Handeni district).

Odontotermes latericius (Haviland).

Although only one nest was located this species is very abundant, foraging in dead wood and constructing earth tunnels up small trees in thicket and bushland. Only an inconspicuous mound is constructed and the sponge-like fungus gardens are superficial. The king and queen were found in a small chamber not far from the surface. Mature alates were caught in flight in October. This flight was observed at 11 a.m. after several days of heavy rain, the alates emerging from small holes in the road where the other castes were congregated. Elsewhere, young alate nymphs were found in December.

Odontotermes ? patruus (Sjöstedt).

There are two records of a few soldiers and workers from bushland, foraging in dry wood and cow dung, at Ngomeni and the Mkomazi valley.

Odontotermes rectanguloides Sjöstedt.

Soldiers and workers have occasionally been found in dead wood on hillsides. This species was also found in the cedar forest of the Western Usambara Mountains and the large mounds aggregated on grey soil around the margin of swampy ground are probably built by these termites (Pl. IX, fig. 2).

Odontotermes stercorivorus (Sjöstedt).

This species has been found occasionally when excavating trenches in red soils. The soldiers and workers occurred in small tunnels at a depth of from 20 to 60 cm.

Odontotermes tanganicus Sjöstedt.

Only soldiers and foraging workers have been found but these are common in dead wood throughout the coastal zone (zone 1). The nest is an inconspicuous mound with clumps of fungus garden near the surface.

Odontotermes zambesiensis (Sjöstedt).

This species is extremely abundant throughout the dry bushland of the whole region. The soldiers and workers are found in dead wood or constructing earth runs over plant litter or up the stems of thicket trees. Excavations have been made but the nest of this species has not been located.

Ancistrotermes latinotus (Holmgren).

A. latinotus is locally abundant in bushland, the soldiers and workers commonly foraging in dry branches on the ground. A strong aromatic smell is characteristic of this species when the soldiers are of a darker orange colour.

Alates were collected in flight in February and October, at about 4 p.m., after several days of heavy rain. They were seen emerging from small holes in the ground with no outward signs of a nest, other than the soldiers and workers lined up round the exit.

The nest has been found in the surface of mounds built by *Cubitermes* and *Trinervitermes*. Fungus gardens are small sponge-like spheres resembling those of *Microtermes* but rather coarser in structure.

Microtermes alluaudanus (Sjöstedt).

This species is very common in bushland and cultivation, foraging in plant litter.

Soldiers are fairly abundant in proportion to the workers. Young alate nymphs have been collected in April and in the last instar in May and October. The mature alates were found, apparently ready for flight, from October to December. Soldier nymphs have been found at all times of the year.

The nest is subterranean, and the fungus gardens are in the shape of small spheres generally aggregated in groups of four or five. The queen occurs in an undifferentiated position below them.

Microtermes magnocellus (Sjöstedt).

This species has been found occasionally, foraging in dead wood near the margin of the Eastern Usambara rain forest. A nest with small spherical fungus gardens was found in the wall of a mound of *Odontotermes* in March. Soldiers, workers and alates were represented.

Microtermes redenianus (Sjöstedt).

This species is abundant in all woodland and thicket on the plains, extending up to an altitude of about 4,000 ft. on the mountain sides.

Fungus gardens have been found at a depth of 50 cm. in light sandy soil, but the remainder of the nest has not been located and only soldiers and workers have been collected.

Microtermes luteus Harris.

Only soldiers and workers are known of this species which appears to be limited to the dry bushland in the northern part of the region. The nest was not located. Specimens were obtained mainly by burying wood pegs in the soil as a bait.

Microtermes vadschaggae (Sjöstedt).

Soldiers are generally very few in proportion to the workers; alate nymphs are found in September and mature alates in April. This species appears to swarm rather later in the season than *M. alluaudanus*.

M. vadschaggae is a widespread species, locally very abundant in dry wood and litter. A complete nest has not been found but fungus gardens have been excavated in red soil at a depth of from 30 to 70 cm.

NASUTITERMITINAE.

Nasutitermes kempae Harris.

Soldiers and workers with alate nymphs were recorded in March. The nest was a loose earthy mound, on red soil, constructed among the roots of a tree. This species is widely distributed throughout the woodland of zone 1, especially among trees of *Brachystegia* and related genera. Runways of red earth are constructed on the boles of trees and over fallen débris, frequently in association with *Microcerotermes*.

Nasutitermes usambarensis (Sjöstedt).

The soldiers and workers are equally abundant. Young alate nymphs have been found in July, and in the last instar in November. Alates were recorded from a different locality in October.

The nest is constructed of a soft carton material adpressed on tree trunks, generally 10 feet or more above the ground. Earth-covered tunnels can usually be traced up and down the tree. No reproductive forms have been found in this arboreal nest, and excavations made at the base of such trees have not revealed a subterranean nest.

This species is associated with tall woodland and forest, but in the rain forest it only occurs near the margin, building tree-top nests on the side having greatest illumination. The soldiers emit a strong resinous smell which is characteristic.

Coarctotermes coarctatus (Sjöstedt).

A rare species found in dry bushland. Alate nymphs have been collected in February and July.

The king and queen have been found in an ill-defined nest consisting of diffuse tunnels in the soil under a log. The small soldiers swarmed over the surface when the colony was disturbed.

Grallatotermes africanus Harris.

The soldiers are of one size and abundant in proportion to the workers. Mature alates and alate nymphs were found within a colony in December.

The nest is a spherical structure of soft black carton-like substance, about 18 in. in diameter, adpressed against a tree trunk and usually over six feet above ground (Pl. IV, fig. 2). The soldiers and the whole colony have a pungent and acrid smell. This species has a strange habit of foraging in long processions, which can be seen leading down the tree trunk and for several yards over the surrounding bushes. They have been observed entering the nest at about midday in cloudy weather. The column is not protected by a tunnel like the other arboreal nasutes, but a covered track may extend for 6 or 8 in. below the nest or for a short distance above it as shown in the photograph.

G. africanus occurs only near the coast, where trees of *Brachylaena hutchinsii* and other species form a very dense woodland.

Trinervitermes rapulum (Sjöstedt).

Small mounds of this species containing major and minor soldiers with workers have been found in woodland on red soils. They are locally abundant.

Trinervitermes segelli (Sjöstedt).

Major and minor soldiers are very abundant among the workers. Mature alates have been found in the nest at most seasons of the year.

The nest is a small hard mound, generally of grey soil, and often extending to a great depth. The queen is only rarely found near the surface. Like other members of the genus *Trinervitermes*, the colony has a characteristic resinous smell.

This is a species associated with grey soils, locally very abundant in patches of grassland and open ground.

Trinervitermes bettonianus (Sjöstedt).

Small mounds of this species are locally abundant on sandy soil, associated with grass tussocks (Pl. V, fig. 1). The colonies contained large numbers of soldiers and workers but no reproductive forms have been found.

Note on the Predatory Fly, *Bengalia floccosa* (Wulp).

The principal predators of termites are the ants, but one other insect is fairly frequent; this is the fly *Bengalia floccosa* (Diptera, CALLIPHORINAE). Professor Buxton drew my attention to this predatory fly which had been observed attacking termites in West Africa. It was therefore of interest to find an apparently similar fly in Tanganyika.

B. floccosa has been observed while making collections in woodland and thicket. On breaking open a termite mound the flies appear within five minutes. Two or three take up a position in view of the digging, and when opportunity offers pounce upon a worker termite with a quick swooping flight, then retreating to a safe distance of one or two feet with the prey. The soldier termites are avoided.

Observations on *Bengalia* have been made in the following localities:

Kahama, Lake Province, attacking *Cubitermes* sp.
Marangu, Kilimanjaro, attacking *Odontotermes* sp.
Handeni district, attacking *Microcerotermes* sp.
Ngomeni, Tanga Province, attacking *Amitermes* sp.
Tanga, attacking *Crenetermes* sp. and *Cubitermes* sp.
Amani, Tanga Province, attacking *Cubitermes* sp.
Daluni, Tanga Province, attacking *Odontotermes latericius* (Haviland).

Bengalia has also been observed attacking a column of the "safari ants" (DORYLINAE). Two flies were observed standing within six inches of a passing column; they remained motionless until an ant larva was being carried past, and then with a quick darting flight snatched the ant and its burden before the protecting soldiers could attack. Alighting at a safe distance from the column, the fly then compelled the ant to drop the larva and made off with the prey, while the worker ant returned to the column. The flies were observed for half an hour, while the ants were crossing a small path in bushland (Kinango, Kenya).

Summary.

The distribution of termites in north-eastern Tanganyika is discussed in relation to eight zones delimited by contours and vegetation types. Some termites show very definite limits to their distribution; *Hodotermes mossambicus* (Hagen) and *Amitermes lonnbergianus* (Sjöstedt) are examples. The significance of this is discussed.

There is a greater variety of TERMITINAE near the coast, while the subterranean termites are the more abundant in dry bushland. Some species are able to extend their distribution where gallery forest is found along the larger rivers. Two types of mountain forest are included in the region and extremely few termites are to be found within these.

The distribution of termites observed on descending from the mountains to

the plains is discussed and illustrated by a diagram. In addition, two methods of indicating the relative abundance of termites in the soil is described.

This is followed by an annotated list of the species collected in the region, giving some account of the castes commonly found and the seasons at which the mature alates have been recorded. For a few species, reference is made to colonies which were established in the laboratory and survived for a few months.

Acknowledgements.

I am indebted to Mr. W. V. Harris, Officer-in-Charge, Colonial Termite Research Unit, for many helpful suggestions throughout the course of this work and for his assistance in identifying the specimens.

References.

Emerson, A. E. (1928). Termites of the Belgian Congo and the Cameroon.—Bull. Amer. Mus. nat. Hist., **57**, pp. 401–574.

Gillman, C. (1949). A vegetation-types map of Tanganyika Territory.—Geogr. Rev., **39**, pp. 7–37, 1 pl.

Harris, W. V. (1936). A list of the termites of Tanganyika Territory . . .—Bull. ent. Res., **27**, pp. 361–368.

Harris, W. V. (1954). Further records of East African termites. II.—Proc. R. ent. Soc. Lond., (B) **23**, pp. 127–137.

Lüscher, M. (1951). Beobachtungen über die Koloniegründung bei verschiedenen afrikanischen Termitenarten.—Acta trop., **8**, pp. 36–43.

Moreau, R. E. (1935). A synecological study of Usambara, Tanganyika Territory, with particular reference to birds.—J. Ecol., **23**, pp. 1–43.

Sjöstedt, Y. (1926). Revision der Termiten Afrikas. 3. Monographie.—K. svenska VetenskAkad. Handl., (3) **3**, no. 1, 419 pp.

Snyder, T. E. (1949). Catalog of the termites (Isoptera) of the world.—Smithson. misc. Coll., **112**, 490 pp.

Wilkinson, W. (1954). Three new species of Kalotermitidae (Isoptera) from East Africa.—Proc. R. ent. Soc. Lond., (B) **23**, pp. 75–82.

Williams, R. M. C. (1954). New East African Termitinae (Isoptera: Termitidae).—Proc. R. ent. Soc. Lond., (B) **23**, pp. 215–227.

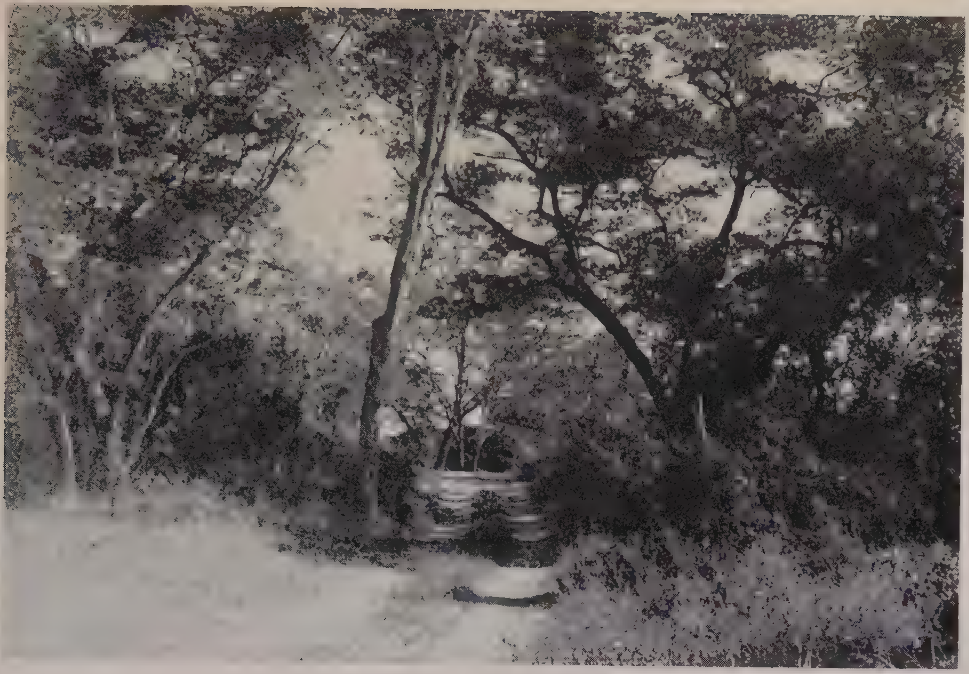


FIG. 1. *Brachystegia* woodland in zone 1.

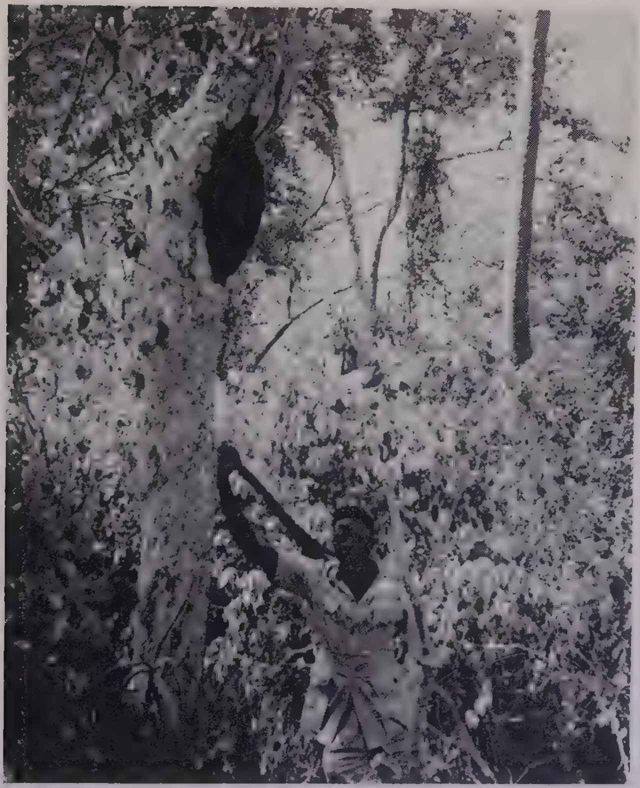


FIG. 2. Arboreal nest of *Grallatotermes africanus* in the dense woodland of zone 1.

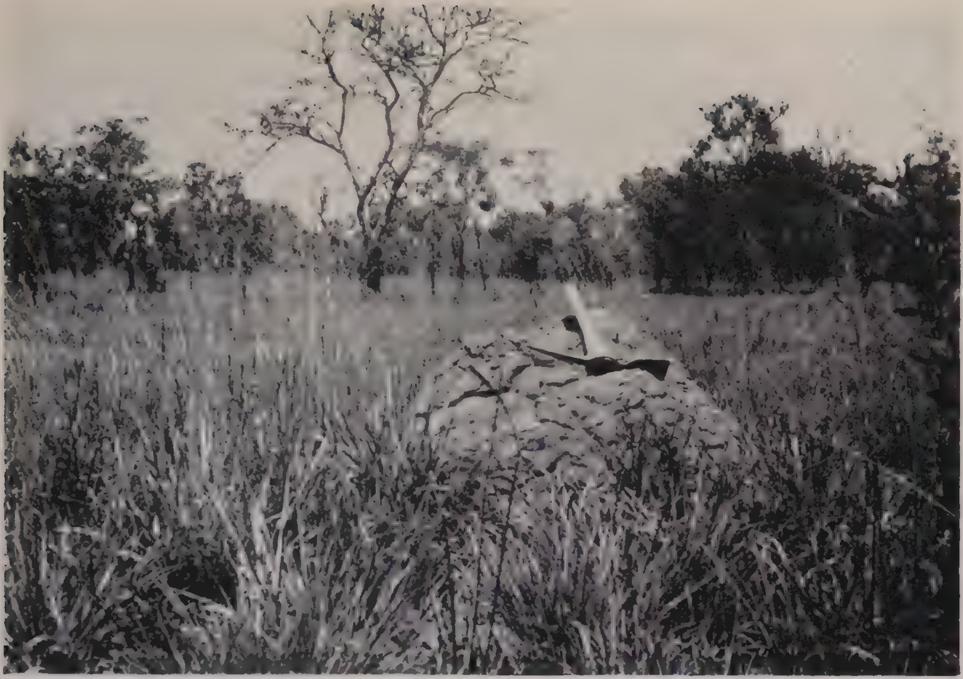


FIG. 1. Thicket and grassland in the Handeni district (zone 1) showing a mound built by *Trinervitermes bettonianus* in the foreground.

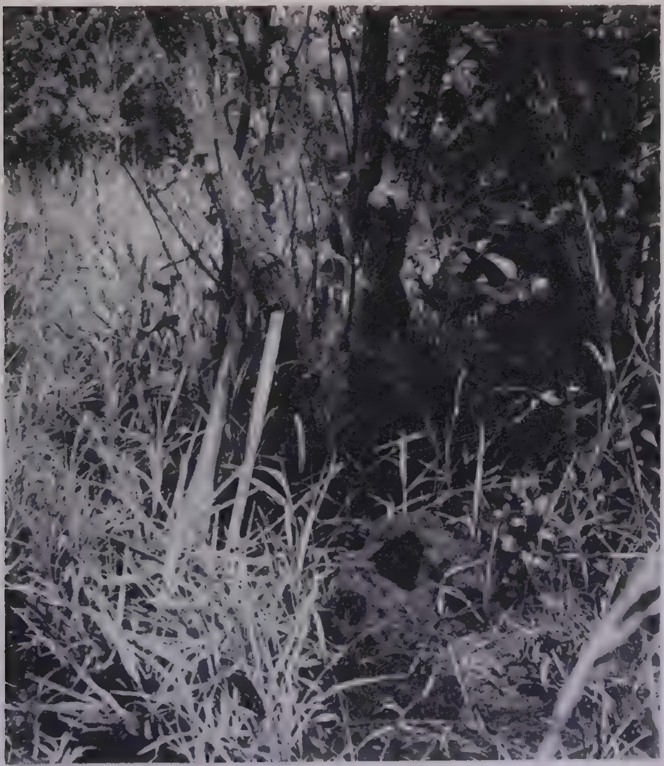


FIG. 2. Dry thicket of zone 1 with a mound of *Odontotermes badius* in the foreground.

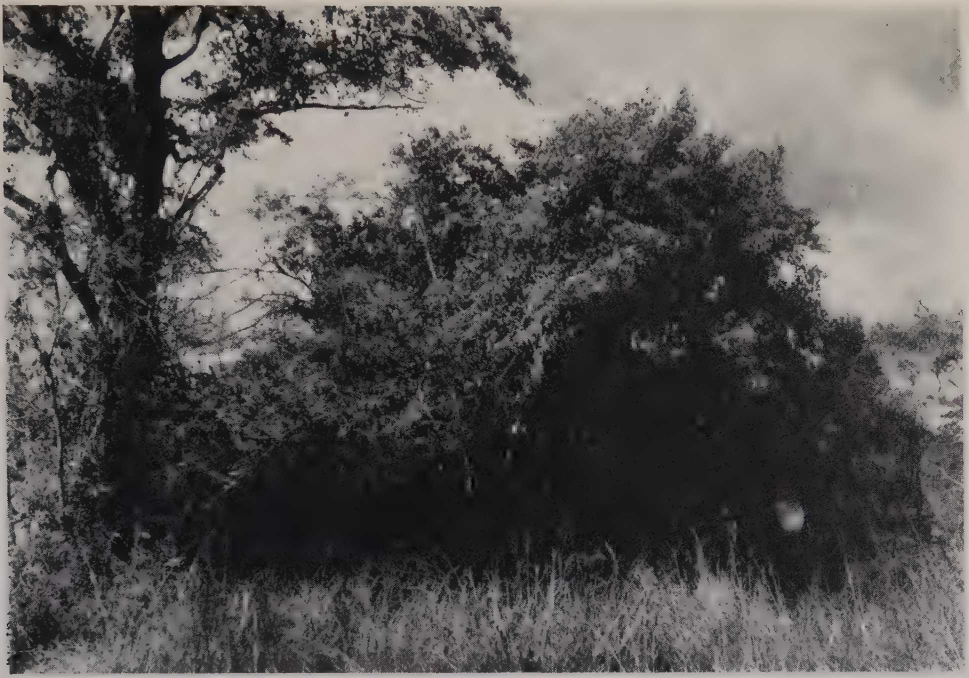


FIG. 1. Grassland in zone 1 with a clump of thicket growing on a mound built by *Macrotermes goliath*.

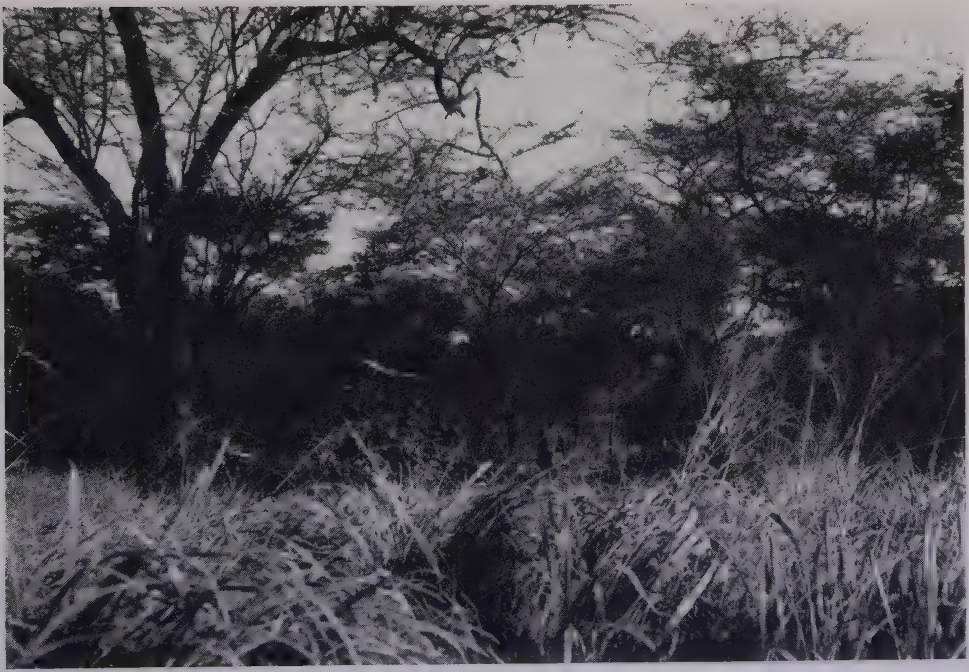


FIG. 2. Bushland of zone 2 seen after the rains. *Acacia—Commiphora* woodland with *Panicum maximum* in the foreground.

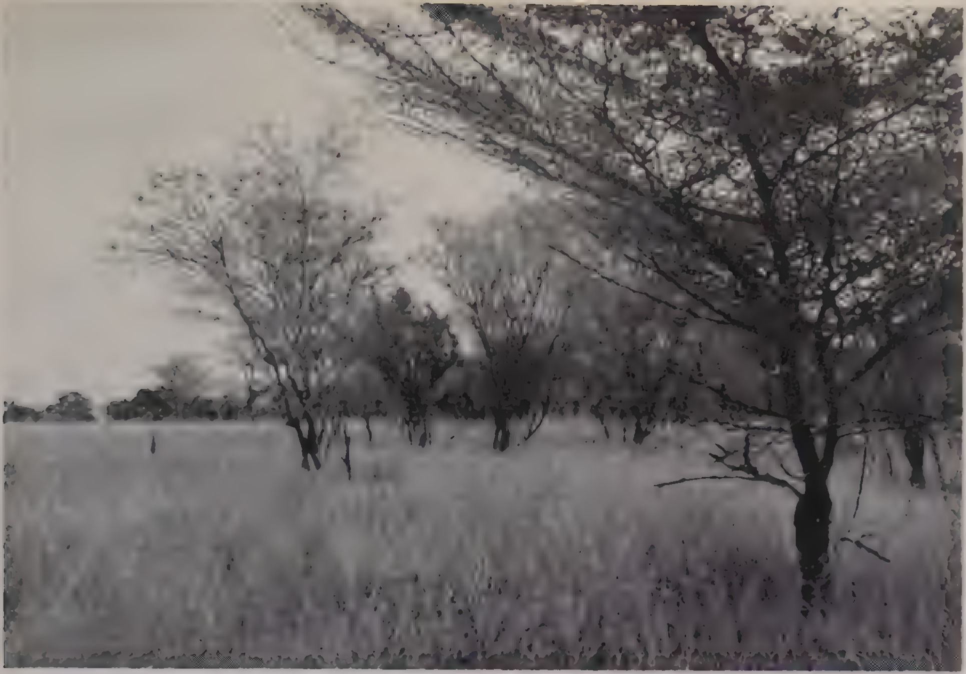


FIG. 1. The zone of *Acacia* woodland on the margin of seasonally swampy grassland in zone 2.

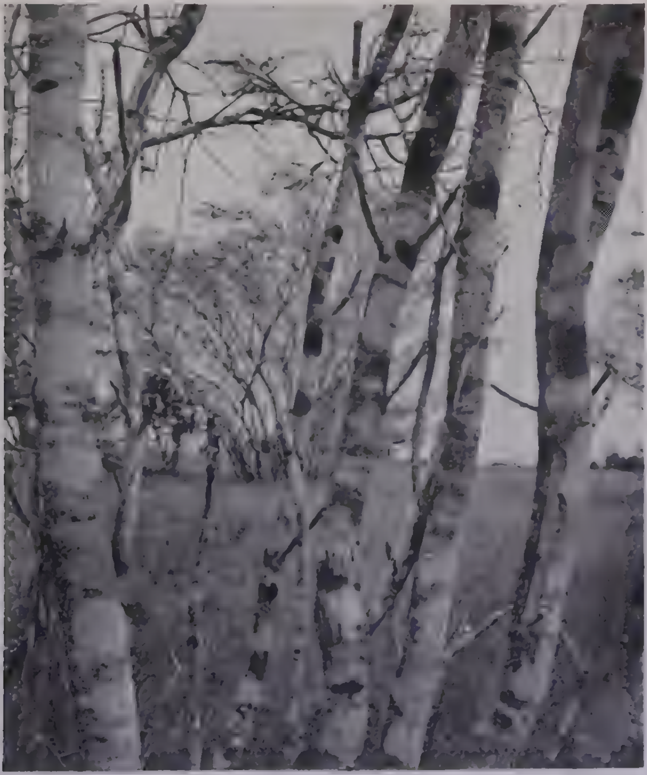


FIG. 2. A detail of the *Acacia* trees shown in fig. 1. The small dead branches were all infested by *Kalotermes kempae.*

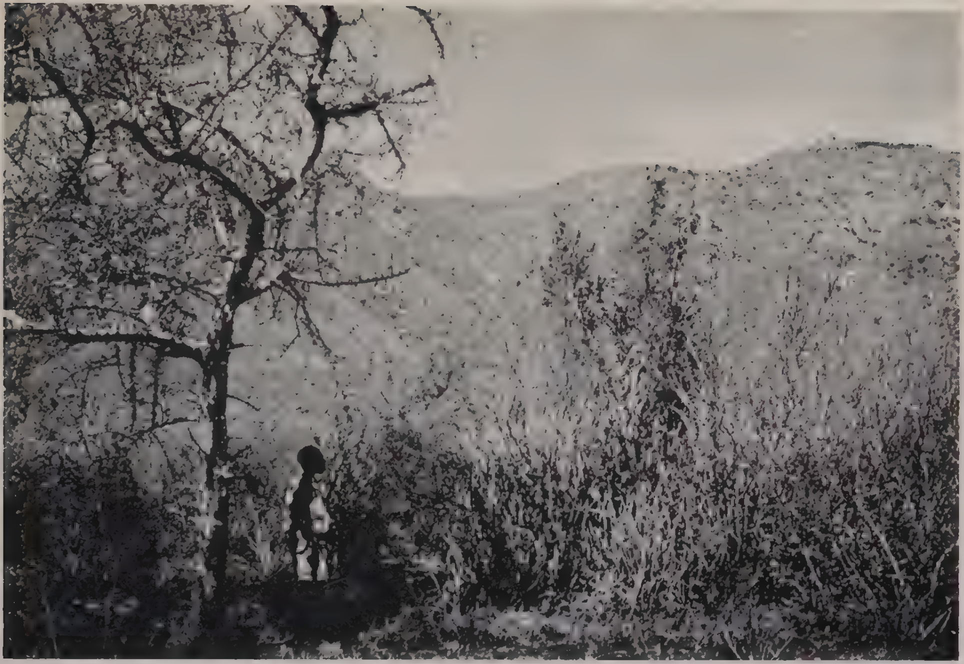


FIG. 1. The very dry *Commiphora* thicket of the Mkomazi valley with the steep wall of the Western Usambara Mountains in the background.

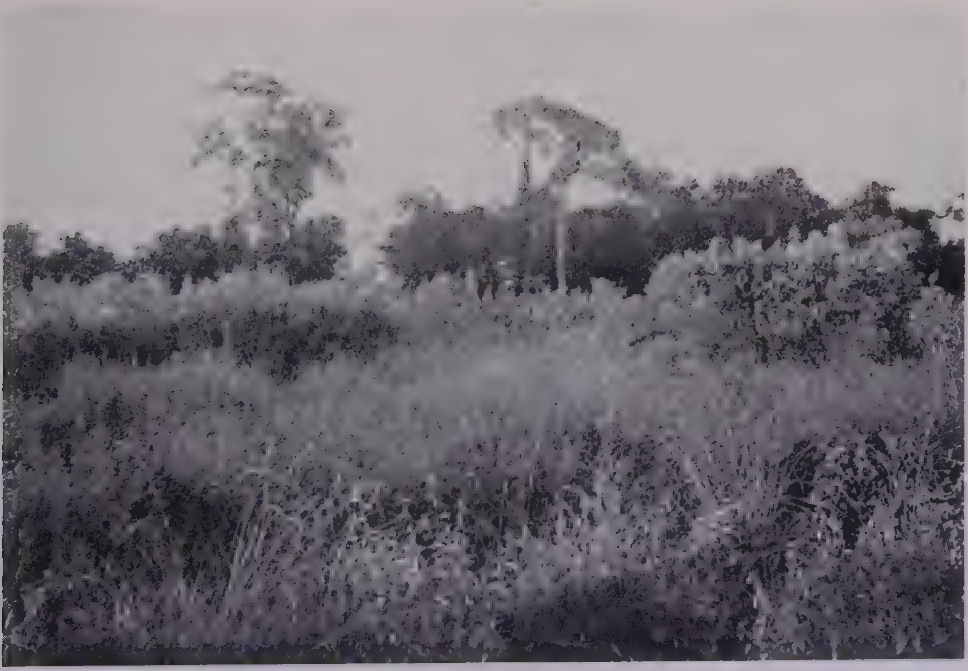
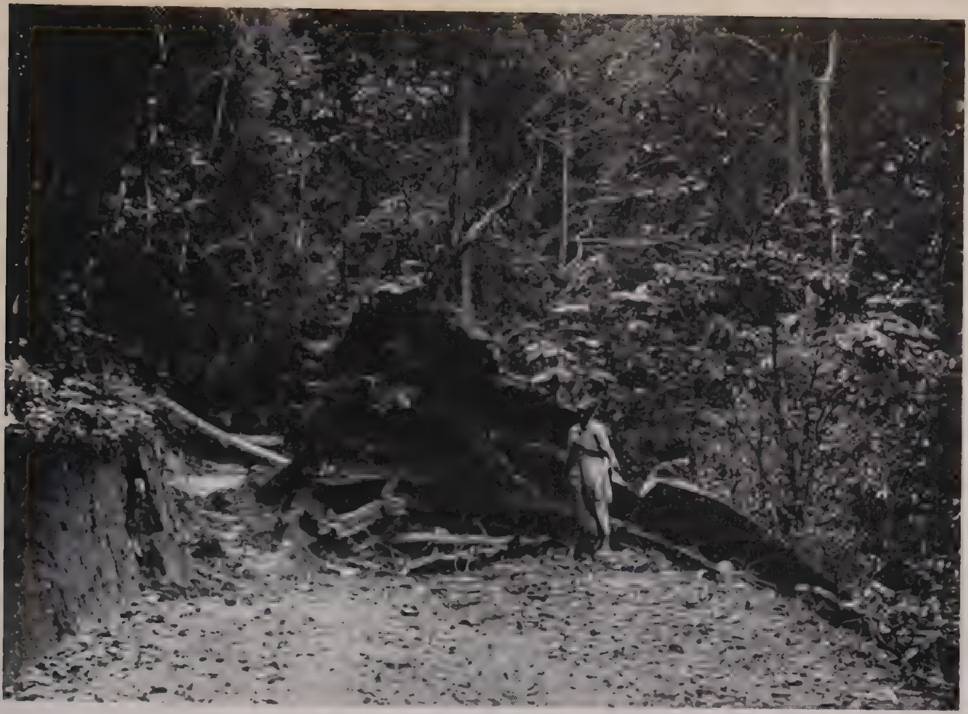


FIG. 2. Tall trees of the riverine forest vegetation (zone 5) with dry scrub in the foreground.



By courtesy E.A.A.F.R.O.

FIG. 1. Tropical Evergreen Rain Forest near Amani (zone 6).

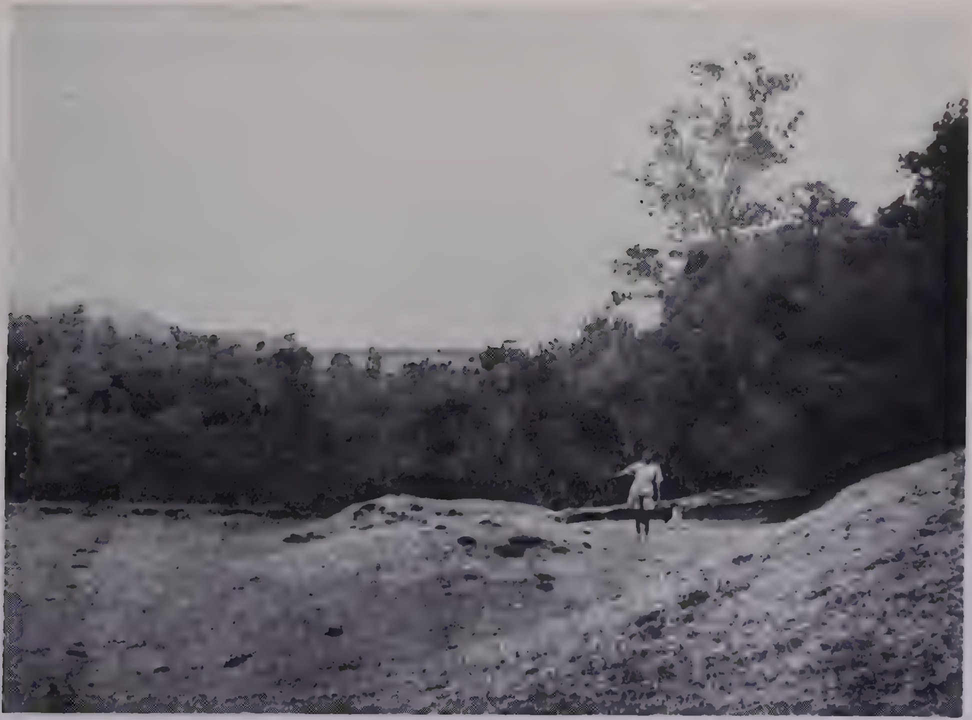


FIG. 2. Large mounds, probably built by *Odontotermes rectanguloides*, in a belt around the margin of swampy grassland. In the cedar forests of Western Usambara (zone 7).

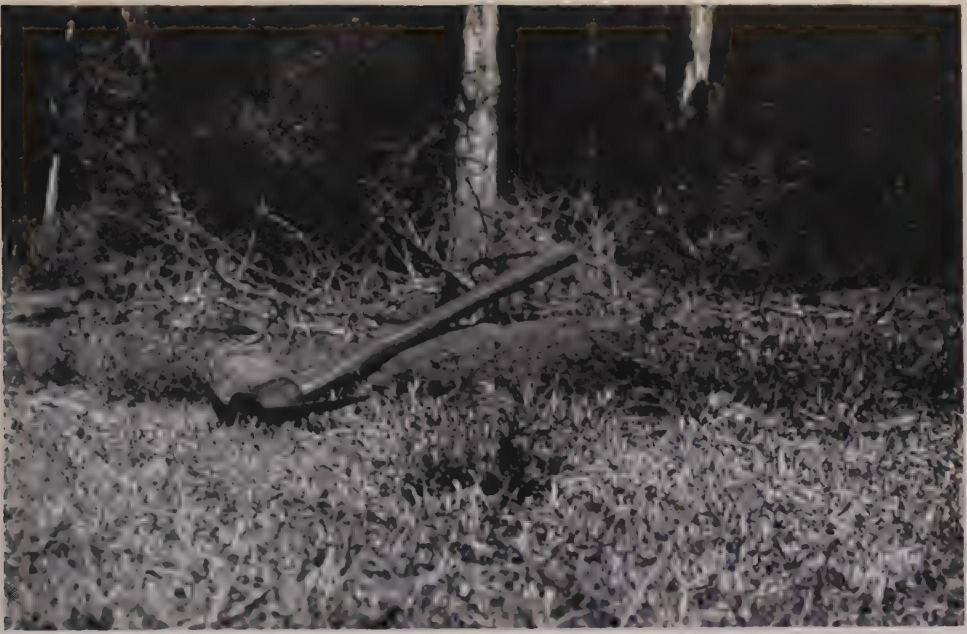


FIG. 1. A mound of *Cubitermes glebae* in a glade of short grassland. The cedar forest in the background (zone 7).

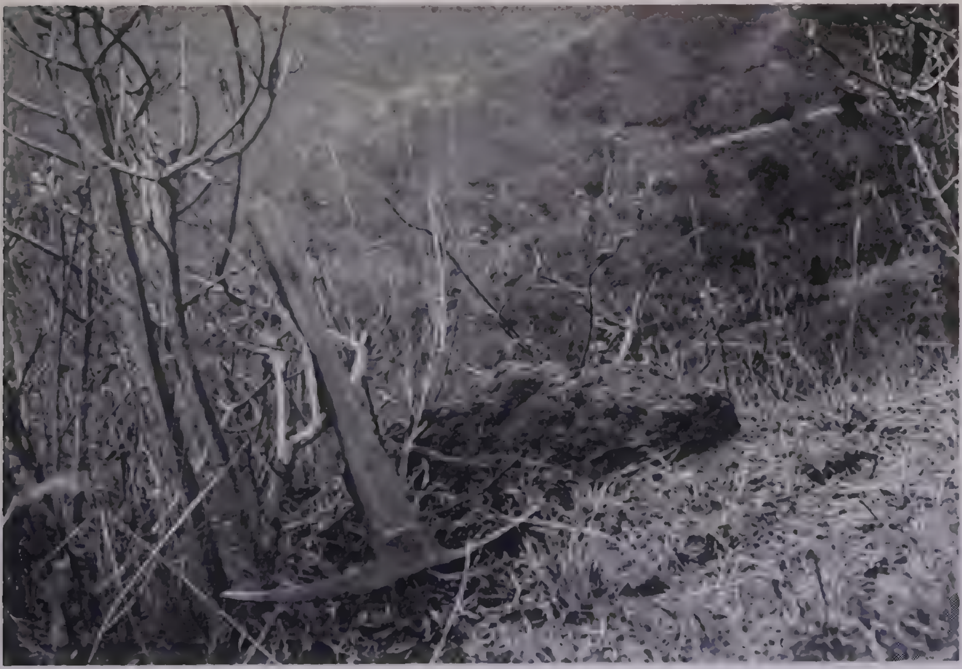


FIG. 2. A mound of *Cubitermes umbratus* on a steep hillside of grazed and eroded grassland. Western Usambara Mountains (zone 8).

ON THE PARASITES AND PREDATORS OF THE COCKROACH.

I.—*TETRASTICHUS HAGENOWII* (RATZ.).

By Ewen Cameron, Ph.D., D.Sc.
Biology Department, St. Mary's Hospital Medical School.

Cockroaches are well-known pests of considerable economic and some medical importance. Up to the present time about twelve hundred species have been described, but only four of these, *Blatta orientalis* L., *Blattella germanica* (L.), *Periplaneta americana* (L.) and *P. australasiae* (F.), are troublesome in Great Britain, and the latter two only occasionally. All four are naturalised aliens. Apart from the damage they do to foodstuffs and other materials, cockroaches are harmful because they are sometimes responsible for the spread of certain diseases of man. For example, they feed, when the opportunity arises, on infective excrement and thus undoubtedly act as mechanical carriers of tuberculosis, cholera, amoebiasis, bacillary dysentery and typhoid. Some species have been under suspicion in connection with the dissemination of leprosy, yellow fever and salmonellosis but, so far, no conclusive evidence has been brought forward to show that they are actual carriers of these diseases. However, the record of their activities is black enough to justify all attempts at their control. Insecticides of various kinds, particularly DDT and γ benzene hexachloride have been used for their suppression with varying degrees of success, but chemicals even when skilfully applied are inadequate when one is dealing with insects which hide away in inaccessible positions beneath floors, behind hot-water piping, enclosed radiators and the many internal recesses of buildings. It is this habit of concealment, amongst other things, which would suggest that the biological method of control might prove a useful auxiliary to the chemical one. The method has been used successfully against many other insects, particularly when, as in the present instance, the pest is of alien origin. It involves the selection, manipulation and deployment of the more important natural enemies of the pest in order to bring its numbers down below the level of economic damage. The natural enemies of the cockroach, mainly parasites and predators, are numerically very abundant, and some of them are very harmful to their host. In the present paper an attempt has been made to deal with all the known enemies of this pest in general, and with one very important parasite, the Eulophid, *Tetrastichus hagenowii* (Ratz.), in particular.

Parasites and Predators of the Cockroach—Group A.

A great variety of organisms from such widely diverse groups as the Protozoa, Nematoda, Insecta, Arachnida, Bacteria and the Algae are associated with the cockroach (" cockroach " used in a collective sense) either as parasites, predators or symbionts. In this paper, and the series to which it is intended to be an introduction, the members of this varied fauna, some 73 in all, are divided into two main groups. From the biological control point of view Group A is the more important one. It contains 37 species of parasites and predators, most of them in the Hymenoptera-Parasitica, together with a few species from other orders. Group B with 36 species, mainly Protozoans and Nematodes, forms an assemblage of lesser interest.

Parasites.

The parasites of Group A fall into three categories, the first belonging to the curious Hymenopterous family of Ensign-flies (EVANIIDAE) and represented by ten species, seven of them in the genus *Evania*; the second belonging to the largest parasitic division of the Hymenoptera, namely the Chalcidoidea with 14 species, mainly from the family EULOPHIDAE (six species), with *Tetrastichus* as the dominant genus, also the ENCYRTIDAE (three species), the PTEROMALIDAE (two species) and the CLEONYMIDAE (one species); and the third belonging to the genus *Rhipidius*, a member of an order (Coleoptera) not much given to parasitism.

In the following Table, which contains 25 species of parasites of the cockroach (all egg-parasites except *Rhipidius*), the host records and geographical distribution of each species are included.

HYMENOPTERA.

Evaniidae.

Evania appendigaster L. ex. *P. americana*, *P. australasiae*, *B. orientalis*, *Bl. germanica*, *Cutilia soror* Brunn., *Neostylopyga rhombifolia* Stoll: Europe (Girault); Palestine (Klein); Fiji (Lever); Hawaii (Swezey); Jamaica (Gowdey); Hungary (Kadocsa); Britain (Crosskey).
Evania dimidiata Spin. (*abyssinica* West) ex. *B. orientalis*: Egypt (Alfieri).
Evania impressa Schlett. ex. *Periplaneta* sp. Fiji (Lever).
Evania laevigata Latr. ex. *B. orientalis*: Europe (Girault); Egypt (Alfieri).
Evania punctata Brullé ex. *B. orientalis*, *Bl. germanica*, *P. americana*: Europe (Fahringer & Cros); Palestine (Klein).
Evania sericea Cam. ex. *P. americana*, *P. australasiae*, *Cutilia soror*, *Neostylopyga rhombifolia*: Hawaii (Swezey).
Evania subspinosa Kieff. ex. *Periplaneta* sp. Fiji (Lever).
Hyptia reticulata Say ex. *Parcoblatta pensylvanica* De Geer: U.S.A. (Rau, 1940).
Brachygaster minutus Ol. ex. *B. orientalis*, *Bl. germanica*, *Ectobius lapponicus* L.: Europe (Girault); Hungary (Kadocsa); also ex. *Ectobius* in England (Nat. Hist.Mus.records).
Zeuxevania splendidula Costa ex. *Loboptera decipiens* Germ.: France (Parker & Thompson).

Eulophidae (Chalcidoidea).

Tetrastichus australasiae Gahan ex. *P. australasiae*: Dutch East Indies (Gahan).
Tetrastichus periplanetae Crwf. ex. *P. americana*: Jamaica (Gowdey).
Tetrastichus hagenowii (Ratz.) ex. *B. orientalis*, *Bl. germanica*, *P. americana*: Europe (Girault); Palestine (Klein).
Tetrastichus sp. ex. *Loboptera decipiens*: France (Parker & Thompson).
Melittobia chalybii Ash. ex. *Periplaneta americana*: U.S.A. (Rau, 1940).
Mestocharomyia oophaga Dodd ex. *Ellipsidion pellucidum* Brunn.: Australia (Dodd).

Eupelmidae (Chalcidoidea).

Anastatus blattidarum Ferr. (*Solendenia blattiphagus*) ex. Cockroach: Sudan (Ferrière); *Blattid* sp.: India (Mani); *Supella*: Arizona (Flock).
Solendenia (*Anastatus*) *picticornis* Cam. ex. *Allacta similis* Sauss.: Hawaii (Swezey).

Encyrtidae (Chalcidoidea).

Comperia falsicornis Gomes. ex. *Supella supellectilium* (Serv.): Hawaii (Anon., 1945).

Cheiloneurus viridiscutum Gir. ex. *Ellipsidion australe*: Australia (Dodd).
Dicarnosis alfierii Merc. ex. *Phyllodromia* (*Blatta*) sp.: Egypt (Mercet).

Pteromalidae (Chalcidoidea).
Pteromalus sp. ex. *Periplaneta americana*: Europe (Girault).
Systellogaster ovivora Gahan ex. *B. orientalis*: U.S.A. (Gahan, 1917).

Cleonymidae (Chalcidoidea).
Agamerion metallica Gir. ex. *Ellipsidion pellucidum* Brunn.: Australia (Dodd).

COLEOPTERA.

Rhipiphoridae.
Rhipidius pectinicornis Thbg. (*Symbius blattarum*) ex. *Bl. germanica*: Hawaii (Van Zwaluwenberg). Also recorded as parasitic on *P. americana* and *Bl. germanica* (Sundevall, in Miall & Denny). This parasite attacks adult cockroaches.

Predators.

The predators of Group A, although not quite so abundant in numbers of species as the parasites, nevertheless add up to an impressive total. First in importance come the members of the Sphecoid genus, *Ampulex*, a group of fossorial wasps which sting and paralyse adult cockroaches and store them in holes and crevices as food for their larvae. Seven species of *Ampulex*, with a distribution ranging from southern Europe to the Far East and America, have been recorded as predators of cockroaches. As well as the Ampulicids, at least two other kinds of insects, a Reduviid and the larvae of a species of *Dermestes* (Coleoptera), also prey on the cockroach. Several members of the Arachnida which do not appear to be of very great importance are also included in this list.

INSECTA.

HYMENOPTERA.

Ampulicidae (Sphecoidea).
Ampulex assimilis Kohl. recorded from *Shelfordella tartara* Sauss.: Iraq (Hingston, 1925).
Ampulex (*Rhinopsis*) *caniculata* (Say) recorded from *Parcoblatta virginica* Brunn. and *Loboptera sakalava* Sauss.: U.S.A. and Canada (Williams, 1929).
Ampulex compressa (F.) recorded from *P. americana* and *Periplaneta* sp.: Oahu, Réunion, Mauritius, India, Burma, New Caledonia (Williams, 1929; Simmonds, 1941).
Ampulex compressiventris Guér. (*siberica*) recorded from " cockroaches ": W. Africa (Sharp, in Williams, 1929).
Ampulex fasciatus Jur. recorded from *Ectobia livida* F.: Mid.- and S. Europe (Picard, in Williams, 1929).
Ampulex ruficollis Cam.: Gibraltar (Williams, 1929).
Ampulex sonnerati Kohl. recorded from " cockroach ": Philippines (Williams, 1929).

HEMIPTERA.

Reduviidae.
Spiniger domesticus Pinto on *P. americana*: Brazil (Pinto).

COLEOPTERA.

Dermestidae.
Dermestes sp. from oöthecae of *B. orientalis*: (Rau, 1924).

ARACHNIDA.

Araneae.
Latrodectus mactans F. recorded as feeding on a heavy infestation of "cockroaches" on board ship at Miami, Florida (Anon., 1939).

Acarina.
Pimeliaphilus podapolipophagus Trägårdh (Piquett & Fales).
Acarus sp. on *B. orientalis* (Miall & Denny).

PARASITES AND SYMBIONTS OF THE COCKROACH—GROUP B.

In this division there are some 36 species, most of them Protozoans or Nematodes, together with one or two rather odd symbionts of little economic importance. The Protozoa are represented by 17 species, two of them from the genus *Endamoeba*, along with various Ciliates and Sporozoans, and the Nematodes by at least 12 or 13 species, mostly from the Oxyuroidea. Also included in this section are various species of bacteria, and bacteria-like bodies found in certain cells in the fat-body, and a rather anomalous associate from the Algae, *Hygrocrocis intestinalis* Val., filaments of which are claimed to have been recovered from the rectum of *Blatta* (Miall & Denny). The more important species of group B are recorded here.

PROTOZOA. Most of these are recorded from the gut of various species of cockroach. *Endamoeba blattae* Butschli; *E. thomsoni* Lucas; *Endolimax blattae* Lucas; *Retortamonas blattae* Bishop; *Hexamita periplanetae* Belar; *Giardia intestinalis* Lambl; *Lophomonas blattarum* S.; *L. striata* Butschli; *Balantidium ovatum* Ghosh; *B. praenucleatum* Kudo; *Plagiostoma* (*Bursaria*) *blattarum* Ghosh; *Nyctotherus ovalis* L.; *Diplocystis schneideri* K.; *Gregarina blattarum* Siebold; *Coelosporidium periplanetae* Lutz & Splend.; *Adelina cryptocerci* Yarwood; *Plistophora kudvi* Sprague & Ramsey.

NEMATODA. *Hammerschmidtiella diesingi* Hamm.; *Leidynema appendiculata* Leidy; *Thelastoma bulhoesi* Magelh.; *T. riveroi* Chitwood; *Blatticola blattae* Graeffe; *Protrellina australasiae* Pessoa & Correa; *P. kunckeli* Galeb; *Oxyuris gracilis* Hamm.; *O. macroura* Dies.; *Filaria rhytipleurites* Desl.; *Gongylonema neoplasticum* Fib. & Ditl.; *Protospirura muricola* Ged.; *Oxyspirura mansoni* Cobbold.

BACTERIA. *Treponema stylopygae* Dobell; *T. parvum* Dobell; *Staphylococcus albus* Rosen.; *Spirillum* sp.; Bacteroids in cells of fat-body (Gier).

ALGAE. *Hygrocrocis intestinalis* Val.

STUDIES OF PARASITES OF THE COCKROACH.

I.—**Tetrastichus hagenowii** (Ratz.).

Systematics, host records and distribution.

This Eulophid (Hymenoptera) (fig. 1) is parasitic on the eggs of the four main species of cockroach. A description of the adult insect is given by Masi

(1917) and also by Burks (1943) who states that: "The body is black with faint iridescent green reflections, areas of head round the mouth-parts, scape and pedicel, tegulae, legs (except procoxae) and sometimes base of gaster white or yellow, the entire supra-clypeal area of the head may be yellow." Perhaps the most striking features of this parasite are the pale straw-coloured eyes, and in the male the long grouped setae on the antennae (fig. 1 *a*). The adults vary in size according to the number of larvae which complete their development in a single oötheca. This number may be as low as ten or less, and as high as 100 or more. Usually, however, about 35 to 40 individuals emerge from an oötheca of *P. americana* and the average length of such adults is for the female, 2·0 mm. and the male, 1·8 mm.

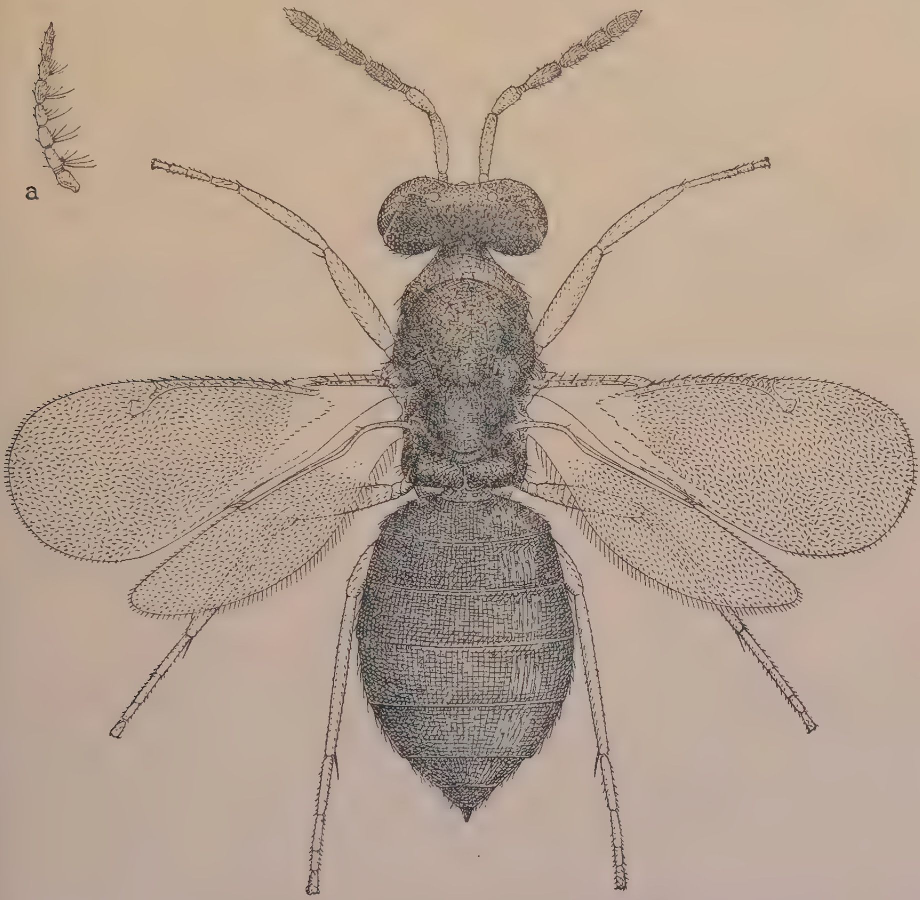


Fig. 1.—*Tetrastichus hagenowii*: female (× 35); *a*, antenna of male (× 35).

Entedon hagenowii Ratz.; *Geniocerus hagenowii* (Ratz.) Kurd.; *Blattotetrastichus hagenowii* (Ratz.) Gir.; *Tetrastichus floridanus* Ashm. and *Tetrastichus browni* Ashm. are all regarded by Burks (1943) as synonyms of *Tetrastichus hagenowii* (Ratz.).

The genus *Tetrastichus* itself is a very large and important one, with a wide variety of hosts amongst the Orthoptera, Odonata, Thysanoptera, Homoptera, Neuroptera, Coleoptera, Lepidoptera, Diptera, Hymenoptera and the Araneae.

Members of the genus have been reared from the eggs, larvae and pupae of other insects, and also from many plant galls. Some species are primary, and others secondary parasites. So far as *T. hagenowii* is concerned, all the specimens reared in the present investigation were direct primary parasites on the eggs of *Periplaneta* spp. There is a reference however in the literature (Lever, 1946) to this species being hyperparasitic on *Evania*, but this is probably an instance of purely accidental competition. The species is not listed by Burks as a hyperparasite.

T. hagenowii has been recorded as a parasite of the oöthecae or egg capsules of *Blatta orientalis*, *Blattella germanica*, *Periplaneta americana* and *P. australasiae*. Its distribution is very extensive, ranging from the Orient to Europe and the Americas. So far it has not been recorded from Great Britain.

General biology.

The material (oöthecae of *P. americana* and *P. australasiae*) on which this investigation was based, came mainly from Trinidad in the British West Indies, and from Saudi Arabia in the Middle East. In the first batch of oöthecae from Trinidad, which arrived in October, the parasites were in the larval stage. By November, the majority of these larvae had completed their development and emerged as adults. They were then transferred to rearing cylinders, and were successfully kept in captivity for periods of up to five or six weeks. A regular supply of water and sugar was provided for them, and the stock was maintained at a room temperature of about 65°F. Oöthecae of *P. americana* obtained from a colony of this species kept in the laboratory were placed in the rearing cages, and the *Tetrastichus* females oviposited in them fairly freely. Eggs and larvae of the parasite were subsequently dissected from the oöthecae. Descriptions of the egg and main developmental stages of the larva and pupa are given below.

In all, some 15 per cent. of the October oöthecae (*P. americana* and *P. australasiae*) from Trinidad were parasitised by *T. hagenowii*, but in a later collection (March) this figure was more than doubled—34 per cent., and in a relatively small sample of *P. americana* the rate was as high as 65 per cent. The Saudi Arabia material (March) yielded a figure of just over 20 per cent. In India, a parasitism rate of 57 per cent. is recorded (Usman, 1949) for *hagenowii* in oöthecae collected during the period July to October, of 43 per cent. in July to December and of 21 per cent. in July to June. These consistently high percentages from such widely separated geographical areas would suggest that this parasite is a very important agent in the biological control of the cockroach.

T. hagenowii is a gregarious or multiple parasite, the average number of adults emerging from a single oötheca of *P. australasiae* being in the region of 40 to 50, and of *P. americana* 30 to 40. Occasionally as many as 70, 89, 110 and in one case the astonishingly high number of 137 living active adults emerged from single oöthecae of *P. australasiae*. In another instance 119 young larvae of *T. hagenowii* were dissected from four out of the 26 cockroach eggs within one oötheca. The distribution of parasite larvae in the infested eggs was as follows, 48, 39, 22 and 10. All the parasitised eggs were on one side of the oötheca and they were arranged in pairs, two in the middle of the capsule, and two near the extremity (39 and 22), (48 and 10).

It is an interesting point that in the genus *Tetrastichus* males are generally rare, and females are usually ten or more times as numerous as the males, while, according to Burks (1943), " In one third of the species of this genus males are unknown, and in some forms males apparently do not exist ". In the present investigation, counts from individual oöthecae gave varying proportions of the sexes, ranging from 50 females to 0 males, 10 females to 1 male, 8 to 1, 4 or 5 to 1, and 5 to 6, but the general average over a large number of oöthecae was about 4 females to 1 male.

Mating took place almost immediately after the parasites were released from the oöthecae into the rearing cages. The males were extremely active and sought out the females with a violent flapping of wings and a quick agitated gait. Prior to copulation the male mounted the female and engaged in preliminary antennal stimulation. This part of the proceedings, in which the male grasped the erect antennae of the female with his own, and appeared to stimulate them by contact and a quivering movement, was momentary, and was quickly followed by the act of copulation. In the cage under observation mating activities were continued for several hours, so that it is obvious that in this particular species of parasite the overwhelming preponderance of females is counter-balanced by the very energetic disposition of the males.

Egg-laying took place soon after mating. The oöthecae were palpated by the female and after much laborious work boring through the tough chitinous wall of the oötheca she deposited her eggs in the egg of the cockroach. As many as 17 eggs of *T. hagenowii* were recovered from a single host egg, and young parasite larvae up to 48 in number were dissected out of one cockroach egg. After hatching, the young larvae fed on the contents of the host egg for a considerable time. Later, they attacked the adjoining unparasitised eggs, and devoured them, until at maturity the original contents of the oötheca had disappeared entirely.

The length of the developmental period of *T. hagenowii* from egg to adult varies according to the temperature. In the laboratory, in England, during the winter months, at an average room temperature of between 60 and 65°F. it is a comparatively long one, eggs laid in the latter part of November not reaching the pupal stage until the end of February or later, and the adults emerging in March, about three months in all. In summer, the development is greatly accelerated. At an average mean temperature of 73°F. (max. 85°F. min. 62°F.) during October and November in India development was completed in less than a month, about 24 days (Usman, 1949). There are several generations of the parasite in a year. In Formosa, where *T. hagenowii* attacks oöthecae of *P. americana* and *P. australasiae* in houses, there are six generations between April and December (Masi, 1917), the life-cycle in that island taking about a month to complete in the hotter summer months, and two months in the period October to December. The duration of life of the adult parasites in the open is unknown, but the period is probably a fairly short one. In captivity, at an average temperature of 65°F., they lived when supplied with water and sugar at regular intervals, for periods of from two to six weeks.

Development.

The egg (fig. 2a) of this species is white in colour, the surface smooth and glistening. It measures about 0·35 mm. in length by 0·08 mm. at the broadest part. In shape it is elongate-oval, slightly arched, and tapering at both ends. Anteriorly it broadens out and terminates in a more pointed extremity. At first its contents are evenly distributed, but as development proceeds the young first-instar larva can easily be seen through the chorion with a clear space at either end of the egg.

The first-instar larva is of the usual Chalcid type, hyaline-white in colour, smooth-skinned apart from some minute spinules on the anterior border of the body segments, fusiform in shape, and consisting of a head and thirteen body segments.

The mature larva (fig. 2b), apart from the increase in size and the prominent dark-brown mass in the gut, is similar in colour and appearance to the earlier stages. In shape it is cylindrical, tapering at either end. The average measurements are 2·7–3·0 mm. in length by 0·8 mm. maximum breadth. Minute spinules are again present, arranged in rows along the anterior border of the body segments. The thirteenth segment is slightly bifurcated posteriorly. There is a well-developed tracheal system with nine pairs of open spiracles (fig. 3c) situated laterally and anteriorly on segments 2 to 10, and two main longitudinal tracheae extending from segments 1 to 11 with anterior and posterior branches to the head and hinder part of the body respectively. The atrium of the spiracle is roughly spherical in shape, 0·02 mm. in diameter, and the spiracular tracheae, especially the first three, are fairly long, and impressed by a series of annular markings just beyond the atrium. Dorsal and ventral branches leave the main tracheae in the region of the spiracular junction.

The cephalic structures of the head (fig. 3a) are important from a diagnostic point of view. They consist of a pair of inverted L-shaped mandibles (fig. 3b)

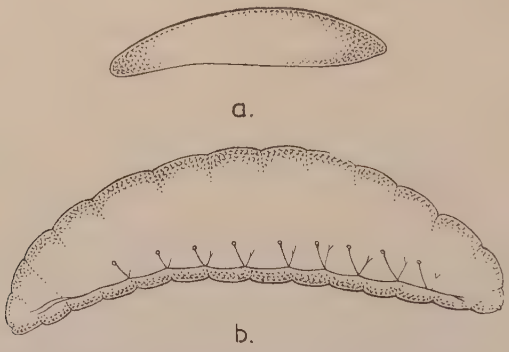


Fig. 2.—*Tetrastichus hagenowii*: *a*, egg (× 100); *b*, mature larva (× 25).

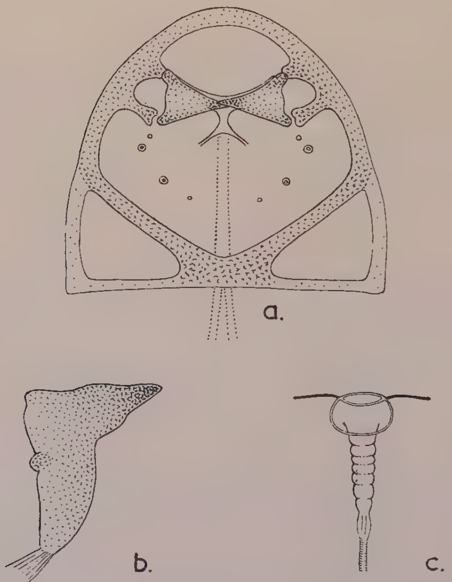


Fig. 3.—*Tetrastichus hagenowii*: *a*, cephalic skeleton of mature larva (× 250); *b*, mandible (× 450) and *c*, spiracle of mature larva (× 400).

strongly chitinised at the tips, and articulating with two projections or rami from the pleurostoma. The pleurostoma itself, which in common with the other cephalic structures is yellowish in colour, is continuous above the mouth and labrum with the arched epistoma and below the mouth with the hypostoma. The two arms of the latter converge towards the mid-ventral surface of the head and fuse well behind the main labial area, thus forming a distinct median sclerite from which, and the hypostoma, lightly-pigmented tentorial rods extend back towards the posterior margin of the head. On the side of the head, ranging out from the median sclerite and the hypostoma, there is a peculiar weakly-developed lattice-like structure which, along with the median sclerite etc., may be of some systematic value. The mouth-opening is surrounded by the labrum, paired mandibles and maxillae, and the labium, none of which has strengthening sclerites. Four pairs of "sensillae", two large and two small, are situated in the area below the mouth bounded by the hypostoma and median sclerite. In this region too the common salivary duct can be traced from its junction below the median sclerite to its opening into the mouth.

Internally the main points of interest are the longitudinal muscle groups arranged laterally, near the outer margin of the body, in four groups of five each; the extensive fat-body with its circular mulberry-like glistening areas; the gut with its narrow oesophagus extending as far as the middle of segment 2, and widening out there to join the greatly distended main gut loaded with dark-brown faecal matter and extending to segment 11. The nervous system is well-developed with a prominent "brain" connected by circum-oesophageal commissures to the ventral ganglia in the head and from there to the ventral longitudinal nerve trunks in the body.

The pupa when newly formed is white in colour. As development proceeds, dark bands appear on the terga of the abdomen and on the anterior part of the thorax, with a few irregular dark patches on the ventral side of the abdomen. Later on the pigmentation becomes more general, and the dark bands become less obvious, until eventually the whole pupa, with the exception of the brilliant orange eyes, assumes a dark brown to black colour. The average measurements of this stage vary from 1·7 to 2·3 mm. in length by 0·6 to 0·8 mm. in maximum breadth. Its duration at a temperature of 65 to 70°F. is roughly about ten days.

Summary.

In this paper the cockroach, a general name used here to include the commoner species of *Periplaneta*, *Blatta* and *Blattella*, etc., is approached from an economic and medical point of view. Special emphasis is placed on the possibilities of its control by biological methods, and to this end the whole field of its inter-relationships with other organisms in various parts of the world has been carefully surveyed. As a result some 73 parasites, predators and symbionts from such widely diverse groups as the Protozoa, Nematoda, Insecta, Arachnida, the Algae and Bacteria have been reviewed and classified.

The more important parasites, some 25 in number, have been placed along with the chief predators in a group (A) by themselves. Most of the former are members of the Hymenoptera-Parasitica, the more prominent being the Eulophid, *Tetrastichus hagenowii* (Ratz.), and the Evaniid, *Evania appendigaster* L., with six of its congeners. Amongst the predators of this group, certain Sphecoid wasps of the genus *Ampulex*, represented by seven distinct species, take pride of place. In the second big division (B) the individual species are mostly members of the Protozoa, with *Endamoeba* as a prominent genus, and of the Nematoda, with several genera, most of them in the Oxyuroidea.

The present paper, which is intended to serve as the introductory one of a series on the natural enemies of the cockroach, deals in detail with a very important parasite, namely the Eulophid, *Tetrastichus hagenowii*.

From the biological point of view this species has great potential value as a controlling agent, being responsible for the destruction of large numbers of cockroach eggs. Oöthecae, which may contain from 16 to 25 or more eggs each according to species, when parasitised by *T. hagenowii* are usually completely emptied of their contents by the developing larvae of this parasite. Parasitism of oöthecae varied from 15 to 34 per cent. in material from Trinidad, and was 20 per cent. in material from Saudi Arabia. A figure as high as 57 per cent. has been recorded from India. On the average some 35 to 40 adult parasites emerge from a single oötheca. A full and illustrated account of the general biology and development of *T. hagenowii* is given, together with notes on its systematic position, host records and distribution.

References.

Anon. (1939). Publ. Hlth Rep., **54,** pp. 2195–2196.

Anon. (1945). Proc. Hawaii. ent. Soc., **12,** 464–465.

Alfieri, A. (1914). Bull. Soc. ent. Égypte, **1913,** pp. 14–15.

Burks, B. D. (1943). Proc. U.S. nat. Mus., **93,** pp. 505–608.

Chitwood, B. G. (1932). Z. Parasitenk., **5,** pp. 14–50.

Cros, A. (1942). Eos, **18,** pp. 45–67.

Crosskey, R. W. (1951). Trans. R. ent. Soc. Lond., **102,** pp. 247–301.

Dodd, A. P. (1917). Trans. roy. Soc. S. Aust., **41,** pp. 344–368.

Fahringer, J. (1922). Z. angew. Ent., **8,** pp. 325–388.

Ferrière, C. (1930). Bull. ent. Res., **21,** pp. 33–44.

Flock, R. A. (1941). Bull. Brooklyn ent. Soc., **36,** pp. 177–181.

Gahan, A. B. (1917). Proc. U.S. nat. Mus., **53,** pp. 195–217.

Gahan, A. B. (1922). Treubia, **3,** pp. 47–52.

Gier, H. T. (1936). Biol. Bull., **71,** pp. 433–452.

Girault, A. A. (1914). Z. wiss. InsektBiol., **10,** pp. 87–91.

Gould, G. E. & Deay, H. O. (1938). Ann. ent. Soc. Amer., **31,** pp. 489–498.

Gould, G. E. & Deay, H. O. (1940). Bull. Indiana agric. Exp. Sta., no. 451, 31 pp.

Gowdey, C. C. (1925). Rep. Dep. Sci. Agric. Jamaica, 1924, pp. 17–20.

Hingston, R. W. G. (1925). Nature at the desert's edge, p. 34.—London, Witherby.

Klein, H. Z. (1933). Z. wiss. Zool., **144,** pp. 102–122.

Kudo, R. R. (1939). Protozoology.—689 pp. London, Baillière, Tindall & Cox.

Laing, F. (1946). Econ. Ser. Brit. Mus. (nat. Hist.), no. 12, 4th edn., 28 pp.

Lever, R. J. A. W. (1946). Agric. J. Fiji, **17,** pp. 9–15.

Lucas, C. L. T. (1927). Parasitology, **19,** pp. 223–235.

Mackerras, I. M. & Pope, P. (1948). Aust. J. exp. Biol. med. Sci., **26,** pp. 465–470.

Maki, T. (1937). Kagaku no Taiwan, **5,** pp. 307–309 (Rev. appl. Ent., (B) **26,** p. 21).

Mani, M. S. (1936). Rec. Indian Mus., **38,** pp. 131–132.

MARSHALL, T. A. (1872). A catalogue of British Hymenoptera. . . —136 pp. London.

MASI, L. (1917). Novit. zool., **24**, pp. 121–230.

MERCET, R. G. (1930). Eos, **6**, pp. 221–228.

MIALL, L. C. & DENNY, A. (1886). Structure and life-history of the cockroach (*Periplaneta orientalis*).—224 pp. London, Lovell Reeve.

MOISER, B. (1946). E. Afr. med. J., **23**, pp. 295–300.

NIGAM, L. N. (1933). Indian J. agric. Sci., **3**, pp. 530–543.

PARKER, H. L. (1924). Ann. Soc. ent. Fr., **93**, pp. 261–379.

PARKER, H. L. & THOMPSON, W. R. (1928). Ann. Soc. ent. Fr., **97**, pp. 425–465.

PINTO, C. (1927). Bol. biol., fasc. 7, pp. 86–87.

PIQUETT, P. G. & FALES, J. H. (1952). Rearing cockroaches for experimental purposes.—U.S. Dep. Agric. Bur. Ent., ET-301, 12 pp.

RAU, P. (1924). Trans. Acad. Sci. St Louis, **25**, pp. 57–79.

RAU, P. (1940). Ent. News, **51**, pp. 33–35, 223–227.

RAU, P. (1944). Canad. Ent., **76**, p. 212.

SHORT, J. R. T. (1952). Trans. R. ent. Soc. Lond., **103**, pp. 27–84.

SIMMONDS, H. W. (1941). Agric. J. Fiji, **12**, p. 26.

SPRAGUE, V. & RAMSEY, J. (1941). Anat. Rec., **81**, suppl., pp. 132–133.

SWEZEY, O. H. (1929). Proc. Hawaii. ent. Soc., **7**, pp. 282–292.

TAUBER, O. E. & GRIFFITHS jr., J. T. (1942). Proc. Soc. exp. Biol. Med., **51**, pp. 45–47.

USMAN, S. (1949). Curr. Sci., **18**, p. 407.

VAN ZWALUWENBERG, R. H. (1946). Hawaii. Plant. Rec., **50**, pp. 11–17.

WENYON, C.M. (1926). Protozoology . . .—2 vols. London, Baillière, Tindall & Cox.

WILLIAMS, F. X. (1929). Proc. Hawaii. ent. Soc., **7**, pp. 315–329.

YARWOOD, E. A. (1937). Parasitology, **29**, pp. 370–390.

ENTOMOLOGICAL STUDIES, RELATING TO YELLOW FEVER EPIDEMIOLOGY, AT GEDE AND TAVETA, KENYA.

By W. H. R. Lumsden
Virus Research Institute, Entebbe, Uganda.

In uninhabited lowland forest in Bwamba County, Uganda, as an example of tropical rain-forest, immunity to yellow fever has so far been found to be widespread only among monkeys; hence it is concluded that these animals are important factors there in the sylvan cycles of transmission of the virus (Haddow, Smithburn & others, 1947). In the same forest the mosquito, *Aëdes* (*Stegomyia*) *africanus* (Theo.), was shown to be the principal vector and insect host of virus during a sylvan outbreak of yellow fever (Smithburn, Haddow & Lumsden, 1949). Although their numbers tend to be reduced during the drier season, adult female *A. africanus* are present continuously throughout the year (Haddow, Gillett & Highton, 1947; Lumsden, 1952) and so persistence of virus appears possible by a simple series of cyclical episodes of transmission from monkey to monkey by *A. africanus*.

Yellow fever virus is known, however, to occur also in areas which yearly experience a prolonged dry season during which adult mosquitos of species of the small-container breeding habit, among which vectors of yellow fever are usually to be sought, appear to be reduced to very small numbers, perhaps sometimes even to complete extinction (Robinson, 1950; Lumsden & Buxton, 1951). Under this condition a simple series of cyclical episodes of transmission from mammal to mammal by mosquitos seems likely to fail. Thus areas subject to a rigorous dry season are increasingly the subject of study to define the mechanism by which virus persists in, or is introduced into, them.

A first study, that of West Nile District, Uganda, has already been reported (Lumsden & Buxton, 1951). The present paper reports the entomological results of two further studies. The field work was carried out in 1951, at Gede from the 24th February to the 19th March, at the end of the dry season, and at Taveta from the 23rd March to the 13th April, in the main wet season. The descriptions of the two areas will to a large extent be given together to save space and to allow easy comparison.

Topography.

Gede (fig. 1) lies on the Kenya coast about 65 miles north of Mombasa; it is mostly low-lying, below 400 ft. in altitude, with gradual slopes. Milne (1936) describes the coastal strip as consisting mainly of loose sands, with black or grey clays occupying low-lying flats, but states that red earths on sandstone, and mottled clays also occur. In the area studied, loose white sand covered almost all the area below 200 ft. altitude, and the boundary between it and a more inland area of fine red earth was very clearly marked; sometimes the transition took place over less than 50 yd. along a road. Some white sand areas occur further inland than the main strip, mainly in the valley bottoms of the red earth area. The soils are, in general, very porous and the only river in the area is the Sabaki which derives its water from inland, mainly from the Athi Plains. The Voi river, to the south of the area, reaches the sea (at the head of Kilifi Creek) only in seasons of exceptional flood (Dale, 1939). The coastline is nearly regular and is of coral limestone. It is broken by the narrow inlet to

Mida Creek (fig. 1). The creek expands inland to an area of white sand which is about five miles long and four broad; much of this sand is uncovered by the sea except at the higher spring tides.

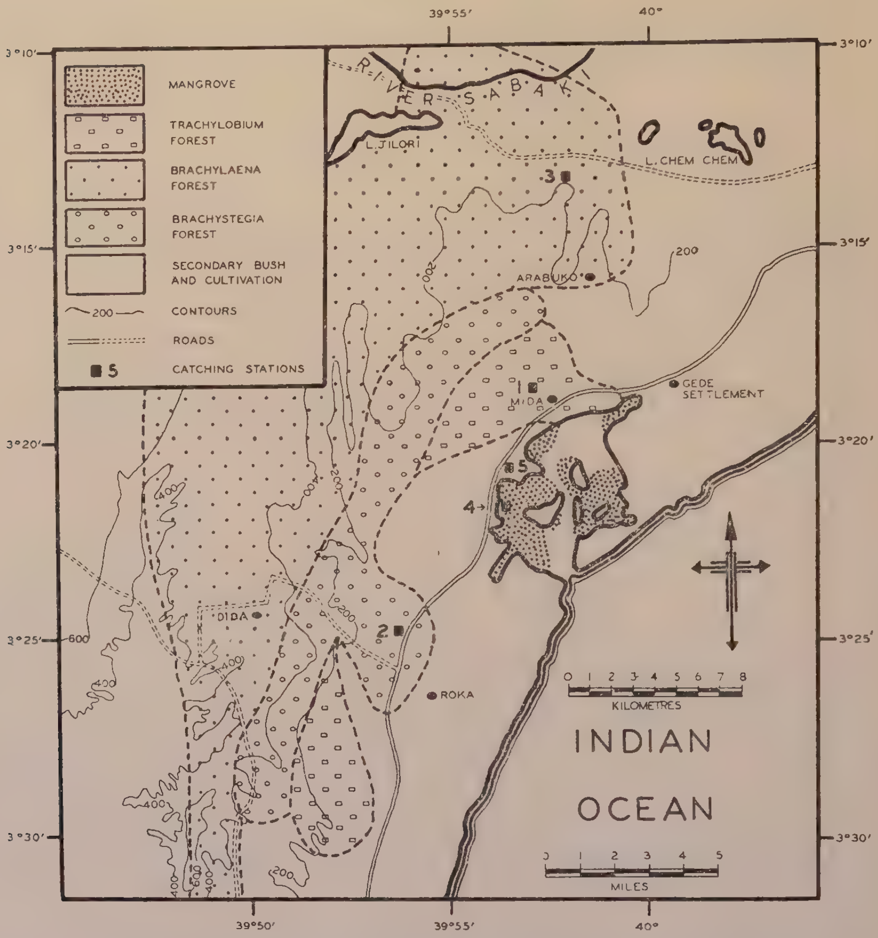

39°55′
40°
3°10′
3°15′
3°20′
3°25′
3°30′
39°50′
MANGROVE
TRACHYLOBIUM FOREST
BRACHYLAENA FOREST
BRACHYSTEGIA FOREST
SECONDARY BUSH AND CULTIVATION
200 CONTOURS
ROADS
5 CATCHING STATIONS
RIVER SABAKI
L. JILORI
L. CHEM CHEM
ARABUKO
GEDE SETTLEMENT
MIDA
DIDA
ROKA
1
2
3
4
5
200
400
600
0 1 2 3 4 5 6 7 8
KILOMETRES
INDIAN OCEAN
0 1 2 3 4 5
MILES

Fig. 1.—Sketch map of the Gede area showing the main features, the distribution of the various forest types, and localities in which work was carried out.

Taveta (fig. 2) lies on the south-east edge of Mount Kilimanjaro about 140 miles from the sea and at an altitude of about 2,500 ft.; it occupies a low pass between the mass of Kilimanjaro to the north and the Pare Mountains to the south. The land slopes generally to the south and east to the Lumi river and Lake Jipe. The Lumi river rises on the east of Kilimanjaro and, running almost due south, passes a short distance to the east of Taveta township. Its flow is augmented just south of Taveta by the discharge of several groups of springs of which the most important are named Njoro and Homer. The Lumi river runs into the north end of Lake Jipe. The Ruvu river, the lake outflow, begins near to the entrance of the Lumi and runs almost due west. A second group of springs, separated from the first by a range of low hills, lies to the south-west, at Kitovu; these springs drain direct to the Ruvu river.

Milne (1936) describes the area as consisting mainly of "plains soils" of the calcareous type with some red earths in the west. There are two patches of volcanic soils, one along the Lumi river and the other at Kitovu (Dale, 1939).

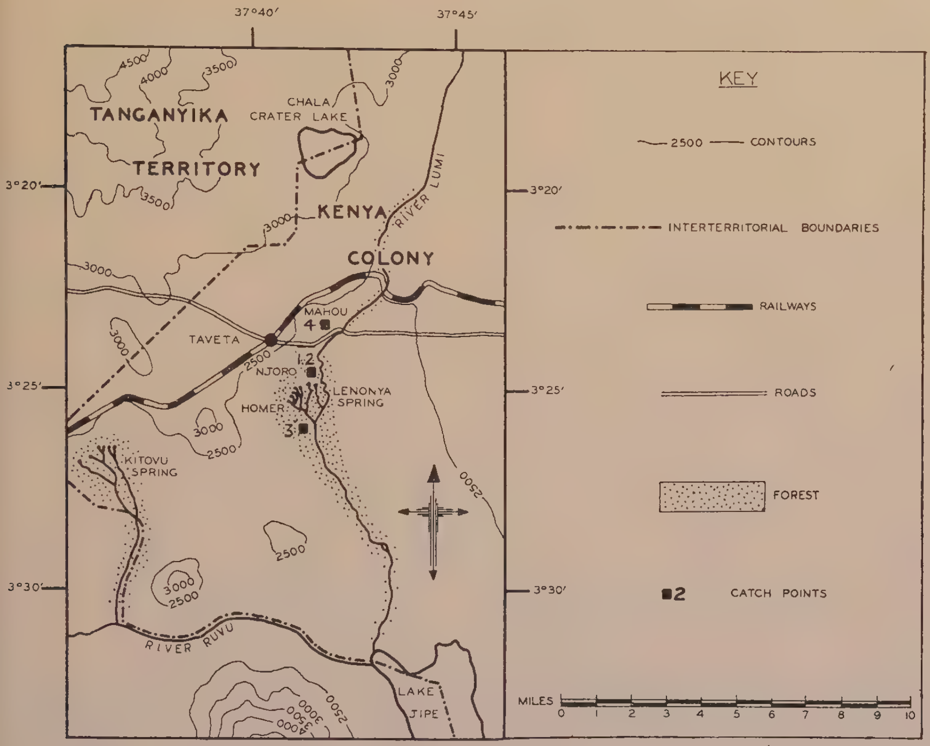

37°40′
37°45′
3°20′
3°25′
3°30′
TANGANYIKA TERRITORY
KENYA COLONY
CHALA CRATER LAKE
RIVER LUMI
MAHOU
TAVETA
NJORO
LENONYA SPRING
HOMER
KITOVU SPRING
RIVER RUVU
LAKE JIPE
1
2
3
4
4500
4000
3500
3000
2500
KEY
2500 CONTOURS
INTERTERRITORIAL BOUNDARIES
RAILWAYS
ROADS
FOREST
2 CATCH POINTS
MILES
0 1 2 3 4 5 6 7 8 9 10

Fig. 2.—Sketch map of the Taveta area, showing the main features and localities in which work was carried out.

Meteorology.

Rainfall records are kept at Gede Settlement but the nearest station at which temperature records are made is Malindi on the coast about ten miles to the north-east. However, Gede is only three miles inland and the Malindi temperatures have been taken as representative also of Gede to construct a climograph of mean daily precipitation and temperature by months (fig. 3).

Temperature variation through the year is small; the mean daily temperature varies only 3·3°, between 24·8°C. (July) and 28·1°C. (April) (fig. 3).

The mean annual rainfall over the years 1941 to 1950 was 36·4 in. (925 mm.) at Gede, slightly more at Malindi, 40·0 in. (1,015 mm.). May is by far the wettest month; its average rainfall over the ten years was 12·2 in. (310 mm.), about one-third of the total annual precipitation. The remaining months were all much drier and none exceeded in rainfall a monthly average of 3·8 in. (97 mm.). The three months January to March are usually the driest ones and at this time the temperature is in the upper half of its range. Figure 3 shows also the conditions by individual months over the most rigorous dry period (1945–46) during the ten years. No rain was recorded at either Gede or Malindi during the three months January to March 1946. Under such conditions it is concluded that the number of breeding sites for mosquitos whose larvae habitually occur in rain-filled tree holes must reach a minimum. The present survey, in February and March 1951, fell at the end of a similar period of drought; no rain was recorded at Gede from the beginning of December 1950, until the end of the work.

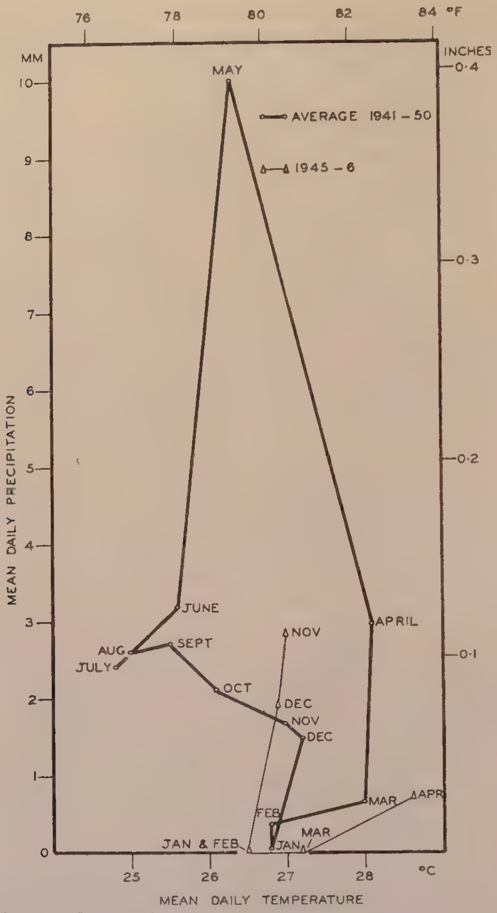


Fig. 3.—Climograph showing mean daily temperature and precipitation at Gede, Kenya, by months. The complete climograph is based on 10 years' records (1941–50); the climograph for the months November to April shows the driest season (1945–6) of the 10-year period.

Rainfall records are kept at a sisal estate at Taveta but the nearest station at which temperature records have been made over a long period is Moshi in Tanganyika about 22 miles to the west and about 200 ft. higher. Temperature records are however, available for Taveta itself for a short period, June 1945 to December 1946, and comparison with the Moshi records for the same months shows that the two places are fairly similar. The mean monthly maximum at Taveta never differed from that at Moshi by more than +2·3 and −0·8°C.; the mean difference was +0·7°C. Similarly, for mean monthly minima the corresponding figures were +2·7, −1·5 and +0·4°C. Moshi is apparently slightly cooler than Taveta, but its figures are taken as sufficiently representative of Taveta also to construct a climograph of mean daily temperature and precipitation (fig. 4).

Temperature variation through the year is much greater than at Gede (*cf.* figs. 3 & 4); mean daily temperature varied 6·4° between 20·4°C. (July) and 26·8°C. (February).

The mean annual rainfall at Taveta over the ten years 1941–50 was 22·6 in. (575 mm.); Moshi is rather wetter, the corresponding figure there being 32·1 in. (815 mm.). The two periods March to May and November and December include most of the rainfall (fig. 4); during the ten years 1941–50, 81 per cent. of the total rainfall fell within them. There are two drier periods, one in January and February when temperatures are near their maximum, and one in the months June to October, which is accompanied by low or moderate temperatures; the latter is the more markedly dry. In other localities so far studied, West Nile District, Uganda, and Gede, Kenya, the driest period of the year was also the hottest. Taveta is an example of opposite conditions in this respect and rain-filled tree holes there may be expected to retain water longer into the dry season than in localities where the hot and dry seasons coincide. Nevertheless, the dry season at Taveta may be both prolonged and rigorous; in the ten years 1941–50 the most pronounced dry season (1943) is shown by individual months in fig. 4. After small falls in June and July, in all amounting only to 0·71 in. (18 mm.), there was no rain for three months.

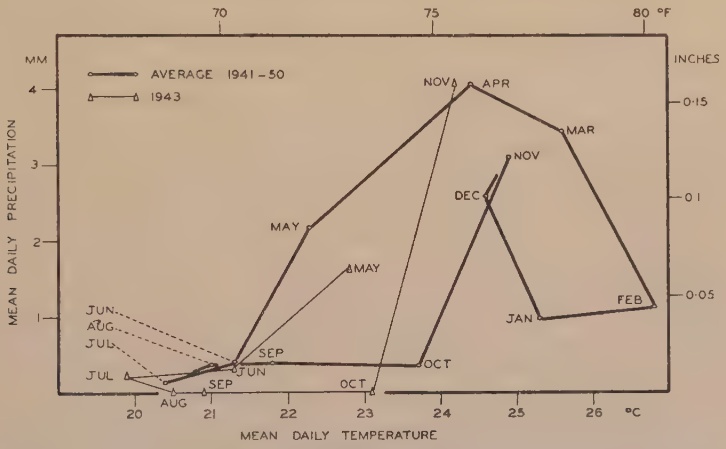


Fig. 4.—Climograph showing mean daily temperature and precipitation at Taveta, Kenya, by months. The complete climograph is based on 10 years' records (1941–1950). The climograph for the months May to November shows the driest season (1943) in the 10-year period.

Vegetation—Gede.

The natural vegetation of the area is discussed in considerable detail by Dale (1939). The approximate distributions of the forest types shown in fig. 1 are mainly derived from him with minor adjustments on my own observations. Brief descriptions of the vegetation types are given below, using Dale's classification:—

Primary woodland.

Mangrove swamp.—Some collections were made at Ras Ngomeni about 24 miles north of Gede, but most of the work was done on the west side of Mida Creek (fig. 1) in mangrove forest which was almost a pure stand of *Avicennia marina*. Besides this species, however, *Ceriops tagal* and *Rhizophora mucronata* were noted nearby.

The *Avicennia* forest is well described as "orchard" mangrove; the trees tend to be regularly spaced and spreading, forming a dense canopy, where the growth is good, at a level of about 6 m. The floor of the forest is moist mud, studded with the pencil-like pneumatophores of the trees. Crab burrows are plentiful, particularly near the bases of the trees.

Lowland evergreen rain-forest, below 1,200 ft.—A forest of this type, near Mida (fig. 1) was investigated. *Trachylobium verrucosum*, *Afzelia quanzensis* and *Manilkara cuneifolia* were all common trees; the environment will be referred to for brevity as *Trachylobium* forest.

This type of forest occurs on loose white sand. It is dense, with much undergrowth of low bushes and a fairly complete canopy at about 10 metres level.

Evergreen dry forest.—Forest of this type was studied mainly near Arabuko but also in other localities, mainly to the south near Dida. The commonest trees were *Brachylaena hutchinsii* and *Cynometra webberi*.

This forest type, which will be referred to as *Brachylaena* forest, occurs on fine red soil at altitudes of 200 to 600 ft. The growth varies considerably but typically the forest is composed of close-set trees of very regular height forming usually a rather open canopy at a level of about 8 m. Undergrowth is very dense and progress through the forest difficult and slow.

Savannah woodland.—This environmental type was studied mainly north-west of Roka where it is traversed by the main road. *Brachystegia oliveri* occurs there almost as a pure stand so that this forest will be referred to as *Brachystegia* forest.

Brachystegia forest occurs mainly as a narrow strip growing on white sand, along the seaward margin of the *Brachylaena* forest but extends downwards to cross the main road near Roka. The trees are large and spreading so that though widely separated they form a complete light canopy reaching up to about 18 m. Undergrowth is scanty and the forest is generally open.

Secondary woodland.

Secondary scrub on coastal sands.—Except for cultivation, which is mainly in the Gede Agricultural Settlement and as small areas associated with the few small villages, and for coconut groves, principally near the sea, the remainder of the area falls into this category. Dale (1939) attributes the variation in the composition of the secondary scrub to different degrees of the factors of rainfall, drainage and fire. Most of this type of country near Gede and Mida is characterised by the presence of baobabs (*Adansonia digitata*) and will therefore be referred to as *Adansonia* bush.

Adansonia bush was studied a little to the south of Mida; it was a dense clothing of bushes and small trees reaching up to about 6 m., with many emergent *A. digitata*; it was sufficiently dense to exclude fire. Much of the secondary scrub is, however, more open and *Hyphaene coriacea* savannah occurs, particularly north of Gede.

Vegetation—Taveta.

The natural vegetation of most of the country is "wooded grassland" or "bushland and thicket" on the classification of Gillman (1949) and is characterised by the presence mainly of *Commiphora* and *Acacia* spp. (Dale, 1939). Near Taveta it is mostly rather open, *i.e.*, in the wooded grassland category. It was studied at Mahou a little to the east of Taveta (fig. 2), where it is better developed than on an average, on account of the proximity of the river.

Dale (1939) describes the Taveta forests in some detail, classifying them as lowland evergreen edaphic forest of a riparian type and listing their main constituent tree species; he states that they occur on volcanic ash in the vicinity of streams and rivers and do not in aggregate cover more than two square miles in area. The present studies were mostly made near Njoro and Homer (fig. 2) but some other localities also were visited. The forest reaches its best development at Njoro where many of the trees exceed 50 m. in stature. At other places in the Lumi valley, and at Kitovu, the trees are smaller though the tree growth is in most places still very good. The canopy is usually fairly complete where the forest has not been touched by man. Undergrowth is generally light.

Population and Cultivation.

Gede.

The population of the Malindi District as a whole may be judged from the records of yellow fever vaccinations carried out during the campaign in 1941 and 1942. These number over 38,000 of which 95 per cent. were of Africans and 3·7 per cent. of Arabs; the remainder was made up mainly of Asians. Those vaccinated at Gede numbered 2,099 of which 2,078 were Africans and 20 were Arabs. The population of the Gede Agricultural Settlement is stated to have been about 1,400 in 1947 so that this number almost certainly includes the surrounding population as well. The African population is mainly of the Giriama tribe; of a total of 104 children interrogated at Penda Kula, Mida, Arabuko and Gede only nine were of other tribes, Sanya, Duruma, Luo and Kambi.

The Agricultural Department Office at Malindi estimates the total area of crops in the District as 17,600 acres. The main crops contributing to this area expressed as percentages, are given as: cotton, 40; maize, 31; cassava, 11; pulses, 9; rice, 4; mtama millet, 3; sweet potato, 2. Bananas are a considerable crop only near the Sabaki river, elsewhere there are only occasional clumps. Coconut palms and cashew, mango and citrus trees are all fairly plentiful.

Taveta.

The indigenous people, the Wataveta, occupy a reserved area along the Lumi river and the frontier with Tanganyika. They were estimated as 2,713 in number in 1929 (Kauntze & Symes, 1933). The area reserved for their occupation includes nearly all of the forest mentioned above. Most of the population lives in grass huts either within the forest or in very close association with it. The most important crop is bananas, which, along with colocasias, are grown in forest clearings, particularly in the vicinity of Njoro. There is a small amount of cultivation in the reserve outside the forested area. Sisal is an important crop outside the native reserve and covers most of the land west of Taveta township.

Methods.

Although both localities are similar in that they are subject to a prolonged dry season, climatic conditions at the time of the visits differed widely; Gede was visited at the end of the dry season, Taveta during the main wet one. However, much the same programme of work was carried out at each place so that comparisons might be drawn. Work in general followed the descriptions given below but sometimes, as will be noted, fewer boys were used, reductions compelled by the difficulty of recruiting labour locally.

The 24-hour catches.

In each locality two catching teams of three native boys were used simultaneously, one catching on a tree platform and one catching on or near ground level. In every case the platforms were well situated among canopy foliage but their level varied considerably depending on the vegetational type being studied.

Each catching team had as a supervisor a boy with long experience in this type of mosquito catching. A senior mosquito boy was in charge of the two simultaneous catches and frequent visits were paid by the writer. The boys caught all insects, that alighted on each other's skins, in small test tubes, plugging the tubes with cotton-wool and depositing them in numbered bags corresponding to the intervals between successive clock hours. The clocks were usually adjusted to a special time, known as " Catch Time ", on which 18 hours coincided with sunset. The necessary clock adjustment was made from East African Standard Time, as known from reliable clocks or watches, by reference to the Nautical Almanac. During the period of the catches the time between sunrise and sunset slightly exceeded 12 hours so that sunrise fell slightly before 0600 hours Catch Time. The discrepancy, however, was trivial; it did not exceed six minutes at Gede and three at Taveta. Only on the first 1½ days of the first catch at Gede was this régime not followed; by an error, the time divisions were at 22 minutes past each hour Catch Time. Only two records of biting insects are affected, and these will be noted appropriately below.

Twenty-four-hour catches were made at Gede in five localities, representative of the main types of environment to be found in the area. The locations (fig. 1) and other details concerning the catches were as follows:—

Catch 1. About 1 km. NNW of Mida; in *Trachylobium* forest; one team at ground level and one at 8·5 m. in a *Manilkara cuncifolia.*

Catch 2. About 3½ km. NNW of Roka; in *Brachystegia* forest; one team at ground level and one at 7·3 m. in a *B. oliveri.*

Catch 3. About 5 km. NNW of Arabuko; in *Brachylaena* forest; one team at ground level and one at 5·2 m. in tree.

Catch 4. About 6 km. SW of Mida on edge of Mida Creek; in *Avicennia* forest; one team near ground level (the ground team sat on a platform about 15 cm. high to be above high tide level) and one at 3·6 m. in an *A. marina.*

Catch 5. About 4 km. SW of Mida; in *Adansonia* bush; one team at ground level and one at 4·1 m. in a small tree.

Besides these complete 24-hour catches a catch by hours was made by 1 to 3 boys on the night 10th-11th March 1951, at Golbanti, in the north near the Tana river.

Twenty-four-hour catches were made at Taveta in four localities, representative of four different environmental types. The locations (fig. 2) and other details concerning the catches were as follows:—

Catch 1. Near the Njoro springs; in high forest; one team (2 to 3 boys) at ground level and one (2 to 3 boys) at 12·7 m. in a *Craibia ? brevicaudata.*

Catch 2. Near the Njoro springs; in banana plantation; one team (3 boys) at ground level.

Catch 3. Near the Homer springs; in high forest; one team (2 boys) at ground level and one (2 boys) at 14·6 m. in a *Balanites ? wilsoniana.*

Catch 4. Mahou, near Lumi river; in wooded grassland, including *Cordia ovalis*, *Ritchiea albersii*, *Acacia mellifera*, *Ficus* spp., *Ziziphus pubescens* and *Grewia* sp.; one team (2 boys) at ground level and one (2 boys) at 5·2 m. in an *Acacia* sp.

The two forest localities (Catches 1 and 3) differed. The forest at Njoro was the wetter and more luxuriant, being composed of giant trees growing in the spring area. At Homer the trees were lower and the ground much drier.

The moving catches.

Haddow (1945) has drawn attention to the greater numbers of mosquitos to be caught in forest on moving as compared with stationary human baits and it was considered that this method might have advantages in discovering adult mosquitos present in only small numbers. Labour was limited but moving catches were made by teams of from 4 to 9 boys within approximately 200 m. of the 24-hour catch sites and in some other environments. Besides catching the insects biting themselves, the catchers inspected the vegetation for resting mosquitos but as most of the boys employed in this sort of work were local recruits with no previous experience of mosquito catching no attempt has been made to separate the results into biting and resting categories. Moving catches were made generally both in the morning and the evening; in the morning they began between 06 and 0730 hours and lasted until between 09 and 12 hours; in the evening they began between 14 and 15 hours and ended between 18 and 1930 hours. The numbers of man-hours of work in each of the environments investigated is given in the appropriate Tables. Six environments were investigated in this manner at Gede, three at Taveta.

Miscellaneous collections.

Although the organised catches described above provided most of the blood-sucking arthropods obtained, these were collected wherever they were encountered and other captures are included here. They comprise miscellaneous catches at human bait, biting insects attracted to vehicles, to light at night, and from shelters, as well as the ectoparasites of mammals. The available information is best arranged under the species of arthropod concerned but will only be recorded if it adds significantly to the knowledge already available from the results of the organised catches.

Collections of mosquito larvae.

At Gede, visited in the dry season, the country was in general very arid and an attempt was made to inspect all persistent waters, possible mosquito breeding sites, and to determine the species produced therefrom. At Taveta, during the rainy season, mosquito breeding places were abundant and little importance was attached to such a general survey, attention being mostly concentrated on breeding places likely to produce vectors of yellow fever.

The mosquito fauna breeding in tree holes was investigated in each of the main environmental types. At Gede, where no naturally water-containing tree holes were found, samples of ten dry tree holes were filled artificially with water, the water was withdrawn one to two days later and the resultant larvae bred up for identification. In *Avicennia* forest the tree holes selected for filling were all over 1·2 m. above ground level so that they might be above the level of the highest tides. At Taveta collections were made from tree holes naturally filled with water.

The importance of plant axils as mosquito breeding places was also studied. At Taveta an attempt was made to define the relative importance of several plants by the examination of standard samples of 50 axils.

It was considered that, besides the adult mosquito catches described above, an additional method of discovering the presence of adult mosquitos was to offer water-filled pots in the several environments and examine them subsequently for eggs or larvae. Both bamboo pots and glass jars were used and before being used they were filled with boiling water which was allowed to stand in them for ten minutes, a precaution necessary to kill any drought-resistant mosquito eggs which they might previously have contained. The pots were placed at various levels in the forests up to a little above the heights of the platforms used. The amount of exposure of pots for each environment may be summarised by "pot-nights", *i.e.*, the number of pots used multiplied by the number of nights on which they were in position. Pots were kept under observation for a minimum of two days after having been brought in from the forest and were inspected daily for eggs or larvae before being discarded as negative. Similar methods were used at both Gede and Taveta, mainly in order to have data from a rainy period to compare with the dry-season results.

Generally, larval collections from tree holes were kept in dishes in the laboratory and pupae taken off and set up for hatching as they appeared. At the end of the visit the remaining aquatic forms were preserved and most of the results of larval identification refer to the collections at this stage. It was inevitable, thus, on such short visits, that the collections were preserved at various times after having been made and that in some of the later ones adults were not obtained. In each larval collection a random sample of 15 larvae was first examined to indicate the approximate representation of each species in the whole collection and, subsequently, the remaining larvae were examined under the binocular microscope and some larvae of each species not represented in the random sample were selected for further examination; it is considered that all the species represented in the collections by mature larvae were thus recognised.

It should be noted that the Gede well water, which was the only water available there for filling both tree holes and oviposition pots, was rather different from rain water. It contained 2,845 parts per million of dissolved solids, probably, as the water was strongly saline to taste, mainly salts derived from the sea.

Species of Biting Arthropods encountered.

Full specific names are given here and abbreviated ones will be used henceforward. The lists for the two localities have been combined to economise space and a capital G or T suffixed indicates that the occurrence was in the Gede or Taveta areas, respectively. An asterisk indicates that the record is made on immature stages, larvae or nymphs. Interrogation marks indicate doubtful records.

HEMIPTERA

REDUVIIDAE

Reduvius planifrons Miller—G.
Platymeris erebus Dist.—G.
Acanthaspis obscura Stål—G.
Oncocephalus sp. indet.—T.

MIRIDAE

Azizus sp. nov.—T.

DIPTERA

CULICIDAE

Anopheles (*Anopheles*) *coustani* Lav. sensu stricto—T.
,, ,, ,, var. *tenebrosus* Dön.—T.
,, (*Myzomyia*) *funestus* Giles—T.
,, ,, *leesoni* Evans—T ?.
,, ,, *rhodesiensis* Theo.—T.
,, ,, *gambiae* Giles—T.
,, ,, *pharoensis* Theo.—T.
Toxorhynchites brevipalpis (Theo.) sensu stricto—T.
Taeniorhynchus (*Coquillettidia*) *metallicus* (Theo.)—T.
,, ,, *maculipennis* (Theo.)—T.
,, ,, *fuscopennatus* Theo.—T.
,, ,, *chrysosoma* Edw.—T ?.
,, (*Mansonioides*) *africanus* (Theo.)—G, T.
Taeniorhynchus (*Mansonioides*) *uniformis* (Theo.)—T.
Aëdes (*Mucidus*) *scatophagoides* (Theo.)—T.
,, (*Ochlerotatus*) *fryeri* (Theo.)—G.
,, (*Finlaya*) *fulgens* (Edw.)—G, T.
,, ,, *ingrami* Edw.—T.
,, (*Stegomyia*) *aegypti* (L.)—G, T.
,, ,, *subargenteus* Edw. sensu stricto—T.
,, ,, *simpsoni* (Theo.)—T.
,, ,, *metallicus* (Edw.)—G, T.
,, ,, *soleatus* Edw.—G*, T.
,, ,, *heischi* van Someren—G, T.
,, ,, *africanus* (Theo.)—T.
,, (*Aëdimorphus*) *haworthi* Edw.—G, T.
Aëdes (*Aëdimorphus*) *ngong* van Someren—G, T ?.
,, ,, *albocephalus* (Theo.)—G, T.
,, ,, *tarsalis* (Newst.) group—T.
,, ,, *tricholabis* Edw.—T*.

DIPTERA—*continued.*

CULICIDAE—*continued.*

Aëdes (*Aëdimorphus*) *cumminsi* (Theo.)—T.
,, ,, *dentatus* (Theo.)—T.
,, ,, *fowleri* (Charmoy)—T.
,, ,, *natronius* Edw.—T.
,, (*Banksinella*) *circumluteolus* (Theo.)—T.
,, (*Diceromyia*) *furcifer* (Edw.)—G, T.
,, ,, *taylori* Edw.—G.
,, ,, *adersi* (Edw.)—G*, T.
,, (*Dunnius*) *michaelikati* van Someren —G, T.
,, (*Skusea*) *pembaensis* (Theo.)—G.
Eretmapodites chrysogaster Graham group—T.
,, *sylvestris* ssp. *conchobius* Edw.—T.
,, *quinquevittatus* Theo. group—T.
,, *oedipodius* Graham group—G*.

Culex (*Lutzia*) *tigripes* Grp.—T.
,, (*Neoculex*) *albiventris* Edw.—T*.
,, ,, *horridus* Edw.—T.
,, (*Culiciomyia*) *nebulosus* Theo.—T.
,, (*Culex*) *poicilipes* (Theo.)—G, T.
,, ,, *aurantapex* Edw.—T.
,, ,, *annulioris* Theo.—T.
,, ,, *sitiens* Wied.—G.
,, ,, *univittatus* Theo.—T.
,, ,, *pipiens pipiens* L.—T.
,, ,, *pipiens fatigans* Wied.—T.
,, ,, *quasiguiarti* (Theo.)—T.
,, ,, *zombaensis* Theo.—T?.
,, ,, *antennatus* (Beck.)—T.
,, ,, *decens* Theo.—G.
Culex spp. indet.—G, T.

CERATOPOGONIDAE
Culicoides adersi I. & M.—G.

TABANIDAE
Chrysops longicornis Macq.—T.
Tabanus taeniola P. de B.—T.
,, *fraternus* Macq.—T.
,, *insignis* Lw.—T.
Tabanus thoracinus P. de B.—T.
,, *par* Wlk.—T.
Haematopota crudelis Aust.—T.
,, *maculosifacies* Aust.—G.

MUSCIDAE
Lyperosia (*Glossinella*) *schillingsi* (Grünb.)—T.
Glossina (*Austenina*) *brevipalpis* Newst.—G.
Glossina (*Glossina*) *pallidipes* Aust.—G.
,, ,, *austeni* Newst.—G.

HIPPOBOSCIDAE
Hippobosca capensis Olf.—T.
Hippobosca struthionis Janson—T.

APHANIPTERA

Xenopsylla crinita J. & R.—G.
Ctenocephalides felis felis (Bch.)—G.
Chimaeropsylla haddowi Smit—G.

ACARINA

Ixodes schillingsi Neum.—T.
,, sp. indet.—G.
Rhipicephalus appendiculatus Neum. —G*, T*.
Rhipicephalus pulchellus (Gerst.)—G*, T.
,, *sanguineus* (Latr.)—G*.
,, *simus* Koch—G, T.
Hirstionyssus liberiensis (Hirst)—G.

Some notes on these determinations are necessary:—

Aëdes fryeri.—Larvae determined as of this species did not agree with Hopkins' (1952) tentative description. However, a collection of larvae, all similar, yielded on breeding out only *A. fryeri* adults (see below). This matter is being investigated.

A. fulgens.—The larvae of this species are indistinguishable from those of *A. longipalpis* (Grünb.). Only *A. fulgens* was obtained as an adult and this species only has been reported from the coastal area of Kenya (van Someren, Teesdale & Furlong, in press), all records are therefore included under this species.

A. ingrami.—The larvae of this species are indistinguishable from those of *A. embuensis* Edw. (van Someren, personal communication) but only *A. ingrami* was obtained as an adult. All records are therefore relegated to *A. ingrami.*

A. subargenteus.—All the four specimens taken were of the type form.

A. soleatus.—The larva of this species may be confused with that of *A. calceatus* Edw. No adults were obtained for confirmation at Gede but only *A. soleatus* occurred among the considerable number of adults obtained at Taveta.

TABLE I.

Summary of the results of 24-hour catches made in the Gede district; February to March 1951.

Catch number	1	2	3	4	5	Total numbers occurring:—				
Environmental type	*Trachylobium* forest	*Brachystegia* forest	*Brachylaena* forest	*Avicennia* forest	*Adansonia* bush	Sunrise to sunset	Sunset to sunrise	On tree platform	At ground level	Totals
Duration of catch (days)	4	3	2	3	2					
T. (*M.*) *africanus*	1					1*			1	1
A. (*O.*) *fryeri*				86	3	27	62	17	72	89
A. (*A.*) *albocephalus*		3		5	4	11	1		12	12
A. (*S.*) *pembaensis*	2	1		95	40	24	114	17	121	138
G. (*A.*) *brevipalpis*	2					1	1		2	2
G. (*G.*) *pallidipes*	7					6	1		7	7
G. (*G.*) *austeni*	3					2*	1		3	3
Totals	15	4	0	186	47	71	181	34	218	252

* One specimen, recorded as taken between sunrise and sunset, may have occurred up to 22 minutes after sunset, owing to error in clock settings (see text).

A. haworthi and *A. ngong*.—Adults of these species from Gede were separated by means of the front tarsal markings which were found reliable in the five *A. haworthi* and seven *A. ngong* males which were dissected so that the identification could be confirmed by the hypopygial details. Larvae examined were not all quite typical of either species so that they have been combined as larval records below. The one female adult from Taveta approached *A. ngong* but five males were all *A. haworthi*.

A. cumminsi.—Of the nine specimens retained for subsequent study, eight were of the ssp. *mediopunctatus* (Theo.); the remaining one approached the type form.

A. natronius.—Only females of this species were available and these are probably indistinguishable with certainty from *A. durbanensis* (Theo.). They are recorded as *A. natronius* as the presence of *A. durbanensis* has not yet been established in Kenya (van Someren, personal communication).

A. furcifer and *A. taylori*.—These species are indistinguishable as larvae in East Africa (van Someren, personal communication). At Gede both species were recognised by the examination of male hypopygia; at Taveta only *A. taylori* was so recognised and all records are therefore included thereunder, but the other species probably also occurs.

Eretmapodites chrysogaster group.—Adult females were probably all *E. intermedius* Edw.; the presence of this species at Taveta has been confirmed by the examination of males (van Someren, personal communication).

Culex albiventris.—The single larva taken agrees with Hopkins' (1952) description of the larvae of this species.

C. nebulosus.—Of five females available for detailed examination, four were of the type form and one was of var. *pseudocinereus* Theo.

C. p. pipiens and *C. p. fatigans*.—These subspecies were separated on the comparative length of the upper fork cell and its stem.

C. zombaensis.—Males are not available for the confirmation of this determination; but the specimens are either of this species or of *C. mirificus* Edw. (van Someren, personal communication).

Results of 24-hour Catches.

The results of the 24-hour catches are summarised in Tables I for Gede and II for Taveta. At each locality some species may be discussed in greater detail.

Gede (Table I).

Taeniorhynchus africanus.—The single specimen taken occurred at ground level between 1722 and 1822 hours Catch Time. No breeding place likely to be used by this species was found nearer than Lake Jilori and the Sabaki river, which at their nearest points approach to within 13 to 16 km. of the catch locality. It seems likely that the specimen came from that area. The vicinity of the Sabaki river was reported as a locality where mosquitos were common and the night catch made at Golbanti near the similar Tana river yielded 313 *T. africanus*, one *T. uniformis* and one *Culex poicilipes*.

Aëdes fryeri.—This species was abundant in the *Avicennia* forest; a few occurred in the *Adansonia* bush. Of the 86 taken in the catch in *Avicennia* forest, 70 (81%) occurred at ground level. The diurnal biting-rhythm of this species is shown in fig. 5.

A. albocephalus.—This species occurred in small numbers in *Brachystegia* and *Avicennia* forests and in the *Adansonia* bush (Table I). All the few specimens were taken at ground level and nearly all by day.

A. pembaensis.—This species did not occur in the catch made in *Brachylaena* forest and was represented by only a few specimens in the catches in *Trachylobium* and *Brachystegia* forests but it was abundant in the *Avicennia* forest and *Adansonia* bush catches (Table I). In these two environments 78 (82%) and 40 (100%) specimens, respectively, occurred in the ground-level component.

Diurnal biting rhythms for this species are shown in fig. 5; they are based on the ground-level component of catches 4 and 5, respectively. The curves for *Avicennia* forest and *Adansonia* bush are shown separately as they are fundamentally different. Specimens biting late in the night, which reach a peak of biting-activity in the hour following sunrise, form a conspicuous feature of the curve for *Avicennia* forest, which is virtually absent in that for the *Adansonia* bush. Although these curves are based on only three and two days' catching, respectively, weather conditions were very regular and do not appear likely to account for this difference. The difference is in accord with the hypothesis advanced by Lumsden (1952) that in insects of this type those which bite during the later night hours are mainly newly hatched specimens whose advent is delayed, probably by mating. This section of the population would be expected to be proportionately more numerous close to the breeding places (*Avicennia* forest) than remote from them (*Adansonia* bush).

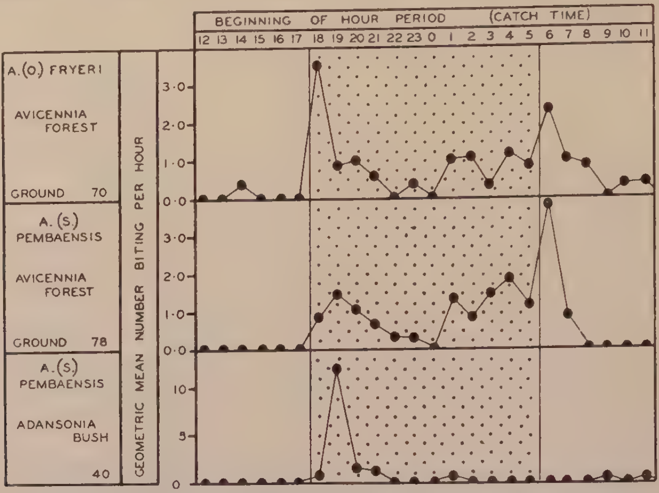


Fig. 5.—The biting-cycles of *Aëdes fryeri* and *A. pembaensis* in the Gede area. The period from sunset to dawn is shown stippled. The total numbers of specimens on which the curves are based are given in the left-hand cells.

Glossina spp.—These insects occurred only in the catch made in *Trachylobium* forest and there only at ground level (Table I). The occurrence of the various species and sexes was as follows:—

		Hour beginning (Catch Time):—								Totals
		05	06	08	09	16	17	18	19	
G. brevipalpis	♂					1				1
	♀	1								1
G. pallidipes	♂		1			1		1		3
	♀		1	2	1					4
G. austeni	♂					1	1			2
	♀								1	1
		1	2	2	1	3	1	1	1	12

Owing to the maladjustment of Catch Time, mentioned above, the *G. austeni* male recorded as occurring in the hour 17–18 (Catch Time) may have occurred up to 22 minutes after sunset.

TAVETA (Table II).

Neither of the genera of Hemiptera recorded bite man habitually and their occurrence in the catches is to be regarded as fortuitous (China, personal communication).

TABLE II.

Summary of the results of 24-hour catches made in the Taveta district; March to April 1951. The insects taken in catch No. 2 are omitted from the comparison of the tree-platform with the ground as this catch was made only at ground level.

Catch number	1	2	3	4	Total numbers occurring:—				
Environmental type and locality	Forest; Njoro	Banana plantation	Forest; Homer	Bush; Mahou	Sunrise to sunset	Sunset to sunrise	On tree platform	At ground level	Totals
Duration of catch (days)	3	1·08	2	3					
Azizus sp.				1		1		1	1
Oncocephalus sp.				1		1		1	1
A. (*A.*) *coustani* s.s.		1		7		8	1	6	8
,, ,, ,, var. *tenebrosus* ..			1	4		5	2	3	5
,, ,, ,, ?var. (damaged) ..			1	2		3		3	3
,, (*M.*) *funestus*	2	2	13	8	8	17		23	25
,, ,, *?leesoni*				1		1	1		1
,, ,, *rhodesiensis*			1			1	1		1
,, ,, *gambiae*	17	139	168	254	92	486	45	394	578
,, ,, *pharoensis*				2		2		2	2
T. (*C.*) *metallicus*				1		1	1		1
,, ,, *maculipennis* .. ♂	1				1			1	1
♀	1					1	1		1
,, ,, *fuscopennatus*	2			6	2	6	3	5	8
,, ,, *?chrysosoma*				1		1	1		1
,, ,, sp. indet. (damaged) ..				1		1	1		1
,, (*M.*) *africanus*	31	3	7	12	8	45	9	41	53
,, ,, *uniformis*	25	1	1	21	4	44	8	39	48
A. (*M.*) *scatophagoides*				2		2	2		2
,, (*F.*) *ingrami*	3		3		6		3	3	6
,, (*S.*) *aegypti*				1	1			1	1
,, ,, *subargenteus* ..			4		4			4	4
,, ,, *simpsoni*	211	107	103	7	414	14	133	188	428
,, ,, *metallicus*				2	1	1		2	2
,, ,, *heischi*				2	2			2	2
,, ,, *africanus*	19				18	1	11	8	19
,, (*A.*) *albocephalus*		2	2	1	5			3	5
,, ,, *tarsalis* gp.	1		2		3			3	3
,, ,, *cumminsi*	12	4	14	2	20	12		28	32
,, ,, *fowleri*				1		1		1	1
,, ,, *natronius*	1			9	4	6	5	5	10
,, (*B.*) *circumluteolus* .. ♂	1					1		1	1
♀	16	1	30	2	39	10	9	39	49
,, (*D.*) *adersi*				1		1	1		1
,, (*D.*) *michaelikati*	1				1			1	1
E. chrysogaster gp.	1	1			2			1	2
C. (*C.*) *poicilipes*				3		3	2	1	3
,, ,, *aurantapex*		1				1			1
,, ,, *annulioris*	1					1		1	1
,, ,, *p. pipiens* and *p. fatigans*	1	6	14	26	2	45	25	16	47
,, ,, *?zombaensis*	3			1		4	1	3	4
,, ,, *univittatus* .. .. ♂	1					1	1		1
♀	2				1	1	1	1	2
,, ,, *antennatus*	7		2			9	4	5	9
Culex spp.	36	8	36	157	8	229	109	120	237
T. insignis	1				1			1	1
TOTALS	397	276	402	539	647	967	381	957	1,614

Anopheles coustani.—Both the type form and the variety were entirely nocturnal and occurred mainly at ground level.

A. funestus.—The species was not taken on the platform. It was mainly nocturnal and, of the eight recorded as occurring between sunrise and sunset (Table II), six were taken in the hour following sunrise.

A. gambiae.—The species was common in all four catch localities except within the Njoro forest where only a few were taken. Of the 439 taken in catches made concurrently on the ground and in the trees, 90 per cent. were taken at ground level. The rhythm of biting-activity was typical, agreeing closely with the curves given by Haddow, Gillett & Highton (1947) and Mattingly (1949). The species was mainly nocturnal, all were taken between 17 and 07 hours except

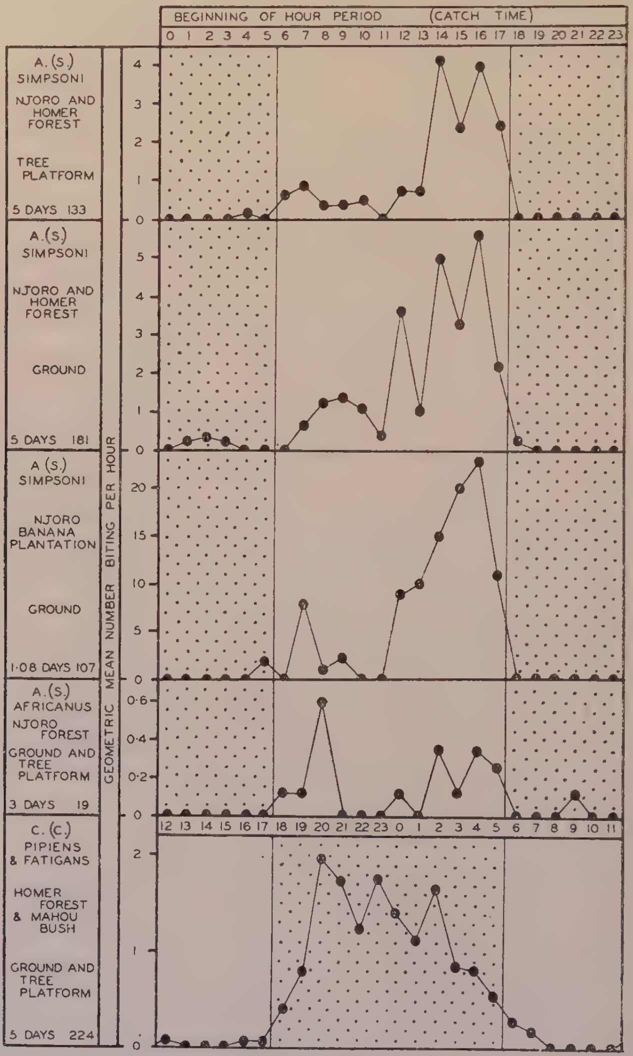


Fig. 6.—The biting-cycles of *Aëdes simpsoni, A. africanus* and *Culex p. pipiens* and *C. p. fatigans* in the Taveta area. The period from sunset to dawn is shown stippled. In the left-hand cells are given the durations of the catches and the total numbers of specimens taken.

for three, at ground level in banana plantations at Njoro, between 09 and 10 hours. The peak of biting-activity was in the hour 04 to 05 hours at both levels.

Aëdes aegypti.—The single specimen taken occurred between 09 and 10 hours.

A. subargenteus.—Only four specimens were taken, all by day at ground level.

A. simpsoni.—This species was common in all four environments save only the bush locality at Mahou (Table II). The species has previously been reported as occurring in forest (Haddow, 1950; Lumsden, 1951*a*) but at Taveta it was more plentiful there than these workers found to be the case in Bwamba, Uganda. Among 40,671 mosquitos taken in forest, Haddow found only 89 *A. simpsoni*. Lumsden, working in an area in Bwamba considered to be one in which *A. simpsoni* was more than usually plentiful, and in forest in close relation to crops suitable for its breeding, took only 22 *A. simpsoni* in a total of 1,225 mosquitos. In Taveta *A. simpsoni* composed 314 (39%) of the total catch of 799 mosquitos in forest environments. The higher prevalence of this species in forest at Taveta is perhaps to be correlated with the prevailing methods of cultivation of bananas. In Taveta the plants are grown in clumps in small forest clearings while in Bwamba they are generally grown outside the main forest although often right up to its edge.

In the two forest environments at Njoro and Homer, 41 per cent. and 46 per cent., respectively, of the total *A. simpsoni* taken occurred in the canopy component of the catch. This agrees closely with the vertical distribution found in Haddow's forest sample (*loc. cit.*) of 89 *A. simpsoni* in Bwamba of which 42 (47%) were taken in the canopy.

By far the greater proportion of the *A. simpsoni* taken was taken by day; only 14 (3·3%) out of a total of 428 occurred between sunset and sunrise. The diurnal biting-rhythm of the species as geometric mean numbers biting per hour for two levels in forest and for banana plantation is shown in fig. 6. This figure may be compared with Haddow's (1945) figures which relate to the behaviour of the species in Bwamba, Uganda. In both series there is an indication of a period of lower activity in the middle of the day but this falls at slightly different times. In Bwamba the midday period of lowest activity is in the hour 13–14, at Taveta (fig. 6) it fell at about 11 hours. A second difference is noted in comparing the levels of activity before and after the midday period of low activity. In Bwamba the two periods are of about equal biting-intensity. In Taveta the morning peak is much less marked than that falling in the afternoon. The finding of these differences has led Haddow (personal communication) to work out a biting cycle for the 89 *A. simpsoni* which he found biting in forest; the curve is closely similar to that now defined for Taveta. Thus this type of curve appears to be characteristic of the species in the forest environment.

A. metallicus.—Only two of this species were taken, in the bush locality at Mahou; both occurred at ground level (Table II), one in hour 11 to 12, the other in hour 20 to 21.

A. heischi.—The species only occurred twice, in the bush locality, at ground level, in the hours beginning 08 and 14 hours.

A. africanus.—Only 19 specimens were taken, all in the forest at Njoro; the occurrence of this important mosquito was as follows:—

Hour beginning (Catch Time)	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	Totals
Tree platform			4						1		2	3				1	11
Ground level	1	1	1				1		2	1	1						8
Totals	1	1	5				1		3	1	3	3				1	19

Although the sample is small, there appear to be certain well-marked differences between the occurrence of this species at Taveta and in Bwamba, Uganda. Firstly as regards vertical distribution, the species was slightly more abundant at the higher level but the difference was only slight; of the total of 19 specimens 11 (58%) were taken at the 12·7 m. level. Haddow, Gillett & Highton (1947) record catches made in the rainy season at two localities, Mongiro and Mamirimiri, in Bwamba, Uganda, with which the present data may be compared. At Mongiro, in ten days catching, three *A. africanus* were taken on the ground and 23 at 31 ft. (10·1 m.), the level nearest to that of the platform used at Njoro; corresponding numbers at Mamirimiri were 17 on the ground and 76 on the platform at 44 ft. (14·4 m.). Thus of the total catches at these pairs of levels, 88 per cent. at Mongiro and 82 per cent. at Mamirimiri occurred on the platform. Even comparing the lowest platforms in each locality in Bwamba, (16 ft. at Mongiro and 22 ft. at Mamirimiri, levels much below the Njoro platform), with the ground, 82 per cent. and 61 per cent. of the catch occurred on the platform in total catches of *A. africanus* of 17 and 44. It appears, therefore, that in Njoro *A. africanus* is comparatively much less plentiful at the upper levels than is the case in Bwamba. Although the Njoro platform was only at about half the height of the average trees it was well situated among foliage on the lower edge of the main canopy.

The diurnal distribution of the specimens taken is shown in the text-table above and as geometrical mean numbers taken per hour per team (both levels combined) in fig. 6. This type of biting-activity curve is quite different from that given by Haddow, Gillett & Highton (1947), and Mattingly (1949) for the species in Bwamba and West Africa, respectively, which shows a low level of biting-activity through most of the 24 hours and a single well-defined period of main activity in the hours about sunset, the peak falling in the hour 18–19. Of the total of 463 specimens taken, 382 (82%) occurred between sunset and sunrise. At Njoro only one of the total of 19 specimens occurred in this period. Most occurred by day and the biting-cycle (fig. 6) much more closely resembles that of *A. simpsoni* with morning and evening periods of biting-activity separated by an interval of low activity between 09 and 14 hours.

Culex spp.—Time was not usually available for the specific sorting of these mosquitos and Table II shows as species only those specimens which were pinned and examined subsequently. The numbers taken on the tree platform and on the ground and by day and by night cannot be compared as they are dependent in part on the numbers pinned and not solely on the natural occurrence of the species. However, separate records were kept of the *C. pipiens*-like species in catches 3 and 4 and of the 42 specimens of this series retained only two were found not to be either *C. pipiens pipiens* or *C. p. fatigans*; they were one *C. zombaensis* and one *C. antennatus*. *C. p. pipiens* and *C. p. fatigans* were about equally represented; in a random sample of 15, 7 showed the upper fork cell less than 3 times the length of the stem (*fatigans*) and 8 exceeded this (*pipiens*). In view of the small representation of other species among the sample of the *C. p. pipiens–C. p. fatigans* series it may be assumed that the numbers recorded for this series are nearly all contributed by these species and advantage may be taken of this to construct a biting-activity curve representative of the species, and also to consider their vertical distribution. Of the totals of 49 and 177 taken at Homer (catch 3) and Mahou (catch 4), respectively, 43 (88%) and 74 (42%) occurred on the platform. The predominance on the platform in catch 3 is probably abnormal; it was contributed mainly by one night (5th–6th April). The hourly totals and the numbers whose identities were confirmed subsequently are shown below:—

The biting-activity curve is shown as geometrical mean numbers biting per team per hour in fig. 6, both levels and catches being combined and the two specimens

Hour beginning (Catch Time)	00	01	02	03	04	05	06	07	12	16	17	18	19	20	21	22	23	Totals
Total recorded	19	17	23	15	13	8	4	3	1	1	1	6	14	36	24	18	23	226
C.p. pipiens or *C.p. fatigans*	3	3	2	3	1	2		1		1		1	3	9	6	2	3	40
Other species													1				1	2

known to be of species other than *C. p. pipiens* or *C. p. fatigans* being omitted. Biting-activity is almost exclusively nocturnal and the main period of activity is between 20 and 02 hours.

Results of the Moving Catches.

GEDE (Table III).

The three main mosquito species, *Aëdes fryeri*, *A. albocephalus* and *A. pembaensis*, were all commonest in the *Avicennia* forest and next so in the *Adansonia* bush. Only *A. albocephalus* and *A. pembaensis* occurred outside these two environments, as occasional specimens in *Brachystegia* forest. It is of interest to compare the relative size of the morning and evening catches of female *A. albocephalus* and *A. pembaensis* in the two environments in which they were common. For comparison, the mean catch per man-hour was calculated from Table III and the evening catch per man-hour is expressed below as a comparative figure, the morning catch per man-hour being taken as unity.

	Avicennia forest		*Adansonia* bush	
	Morning	Evening	Morning	Evening
A. albocephalus ..	1	0·09	1	2·06
A. pembaensis ..	1	0·10	1	1·45

This relation is, for *A. pembaensis*, parallel to and confirmatory of the effect which has already been noted in the discussion of the 24-hour catches. The existence of a similar relation in *A. albocephalus*, together with the comparative sizes of catches of this species in the several different environments, is indicative that the breeding places of this species in the Gede area are also associated with the sea.

Three species of *Culex* occurred as single specimens in the *Avicennia* forest. *C. sitiens* and *C. pipiens fatigans* have both been recorded as breeding in sea water (Hopkins, 1952). *C. univittatus*, however, is generally considered to be a species preferring fresh water. Kirkpatrick (1925), working in Egypt, examined 384 samples of water in which the species (referred to as *C. perexiguus* Theo.) was found as a larva; in no case did the salinity observed exceed 6·1 parts Cl in 1,000 of water. The sea averages 19·3 parts Cl per 1,000 of water (Murray, 1913). A few open wells are to be found on the edges of the creek and, though no breeding was found in those inspected, it seems most likely that this mosquito came from them.

The moving catches obtained *Glossina* spp. in all the forest environments except the *Avicennia* forest.

TABLE III.

Summary of the results of moving catches in the Gede area: March 1951.

Environmental type		*Trachy-lobium* forest		*Brachystegia* forest		*Brachylaena* forest		*Avicennia* forest		*Adansonia* bush		Cultivation	Totals
Morning or evening		M	E	M	E	M	E	M	E	M	E	M	
Man-hours of catching		60	15	17	22	40	40	37	67	40	21	14	373
A. (*O.*) *fryeri*	♂								2				2
	♀							38	17		1		56
A. (*A.*) *albocephalus*	♂								1				1
	♀			1	1			24	4	12	13		55
A. (*S.*) *pembaensis*	♂							2					2
	♀				1			476	163	25	19		684
C. (*C.*) *sitiens*	♀								1				1
C. (*C.*) *univittatus*	♀								1				1
C. (*C.*) *pipiens fatigans*	♀								1				1
G. (*A.*) *brevipalpis*	♂				1								1
	♀						1						1
G. (*G.*) *pallidipes*	♀	1											1
G. (*G.*) *austeni*	♀		1		2								3
Totals		1	1	1	5	0	1	540	190	37	33	0	809

TAVETA (Table IV).

A few additional remarks may be made:—

Taeniorhynchus metallicus and *T. maculipennis*.—These two species were common, respectively, in the bush at Mahou and in forest at Njoro. They were but little represented in the 24-hour catches on stationary bait.

TABLE IV.

Summary of the results of moving catches in the Taveta area: March to April 1951.

Environmental type and locality		Forest; Njoro		Forest; Homer		Bush; Mahou		Totals
Morning or evening		M	E	M	E	M	E	
Man-hours of catching		24	15	12	12	12	12	87
T. (*C.*) *metallicus* ..	♂					15		15
	♀					10	3	13
,, ,, *maculipennis* ..	♂	5	12					17
	♀	2	4					6
,, ,, *fuscopennatus* ..	♀						2	2
,, (*M.*) *africanus* ..	♀	1	1					2
,, ,, *uniformis*	♀	1						1
A. (*F.*) *fulgens*	♀	1				1		2
,, (*S.*) *aegypti*	♂					1		1
,, ,, *simpsoni*	♀	4	16	4	6	1	1	32
,, ,, *soleatus*	♀	1				3		4
,, ,, *heischi*	♀						1	1
,, ,, *africanus* ..	♀		1					1
,, (*A.*) *albocephalus* ..	♂			1				1
	♀	3		3		17	1	24
,, ,, *tarsalis group* ..	♀			2		1		3
,, ,, *dentatus*	♀		1					1
,, ,, *tricholabis* ..	♀					1		1
,, ,, *cumminsi*	♂			2				2
	♀	3		6	7	4		20
,, ,, *natronius* ..	♀						6	6
,, (*B*). *circumluteolus* ..	♂				4	1	4	9
	♀	7	3	6	8	1	7	32
,, (*D.*) *michaelikati* ..	♂	1						1
	♀					1		1
E. chrysogaster group ..	♀	1				1		2
,, *sylvestris* ssp. *conchobius*	♀				1			1
C. (*L.*) *tigripes*	♂	1			1	1		3
	♀			1	1			2
,, (*C.*) *univittatus* ..	♂			4	3	1		8
	♀			2	2			4
,, (*C.*) *pipiens fatigans* ..	♂			1				1
,, (*C.*) *quasiguiarti* ..	♂		1					1
Culex spp. indet.	♂		2	9	6	2		19
	♀			1	3	1	3	8
Totals		31	41	42	42	63	28	247

Aëdes aegypti.—Only a single specimen was taken, in the bush environment, which also was the only environment which yielded the species in the 24-hour catches. It was found, however, to be present as a larva in tree holes in the forest (see below).

A. simpsoni.—This was the only *Stegomyia* taken in any considerable numbers and was again more plentiful in forest than in the bush locality.

A. soleatus, *A. heischi* and *A. africanus*.—Represented by only occasional specimens.

Miscellaneous Collections.

Reduvius planifrons, *Platymeris crebus*, *Acanthaspis obscura.*—Occasionally attracted to light by night; not taken biting (Gede).

Aëdes fryeri.—Common biting man, *Avicennia* forest, evening (Ras Ngomeni, 24 miles north of Gede).

A. aegypti.—Two females found resting in native houses (Gede Settlement).

A. pembaensis.—Common resting in the mouths of the burrows of the crab, *Sesarma* (*Holometopa*) *culimene* de Man., in *Avicennia* forest; of seven females collected three had had recent blood-meals and two were gravid (Gede; Mida Creek). Common biting man in *Avicennia* forest, evening (Ras Ngomeni).

Culicoides adersi.—Common biting man in coconut grove near creek, evening (Gede; Mida Creek).

Haematopota maculosifacies.—Females attracted to stationary motor vehicles by day, commonly in *Brachystegia* forest, occasionally in *Trachylobium* and *Brachylaena* forest (Gede; Mida and Arabuko).

H. crudelis.—Two females attracted to stationary vehicles in forest (Taveta; Kitovu).

Tabanus fraternus, *T. par*, *T. taeniola* and *T. thoracinus.*—Females attracted to stationary vehicles by day in open bush country; the first two species the most common (Taveta).

Lyperosia schillingsi.—Biting man by day in open bush (Maktau, about 30 miles east of Taveta).

Glossina brevipalpis.—One male and three females attracted to motor vehicles at dusk in forest (Gede; Mida and Arabuko).

G. pallidipes.—One female attracted to vehicle in *Brachystegia* forest (Gede; near Roka).

Hippobosca capensis.—On dog (Taveta).

H. struthionis.—On *Gazella* (*Nanger*) *granti petersi* (Grant's gazelle) (Maktau). The species has been considered a strictly specific parasite of the ostrich (Holroyd, personal communication).

Xenopsylla crinita.—On *Cricetomys gambianus osgoodi* (giant rat) (Gede).

Ctenocephalides felis felis.—On *Petrodromus sultani sultani* (elephant-shrew) (Gede).

Chimacropsylla haddowi.—On *Rhinonax chrysopygus* (elephant-shrew) (Gede). This flea, a new species, is described by Smit (1952).

Ixodes schillingsi.—One female from man (Taveta; Njoro).

Ixodes sp. indet.—One nymph from *P. s. sultani* (Gede).

Rhipicephalus appendiculatus.—Nymphs, probably of this species, from *Rhinonax chrysopygus* and *P. s. sultani* (Gede), and from *G.* (*N.*) *g. petersi* (Maktau).

R. pulchellus.—Nymph, probably of this species from *P. s. sultani* (Gede). Adults from *G.* (*N.*) *g. petersi* and from man (Maktau).

R. sanguineus.—Nymphs, probably of this species, from *P. s. sultani* (Gede).

R. simus.—Nymph, probably of this species, from *P. s. sultani*; adults from *Papio doguera ibeanus* (baboon) (Gede). On man (Maktau).

Hirstionyssus liberiensis.—From *Heliosciurus undulatus daucinus* (squirrel) (Gede).

Eight hollow trees in *Brachystegia* forest (Gede; near Roka) were searched for biting insects by means of smoking; none was found.

Larval Collections.

General.

Extensive searches in the Gede area failed to discover any naturally water-filled tree holes or leaf axils and led to the conclusion that the only waters available in the dry season for mosquito breeding were sea inlets, the River Sabaki and Lake Jilori, water pits and wells and domestic water containers. At Taveta breeding places were abundant. Notes on species taken in collections of this general sort follow and certain special larval environments will be discussed separately later.

Aëdes fryeri.—Larvae common in saline water a few cm. deep over white sand (Gede; Mida Creek).

A. aegypti.—Common as a larva in domestic water containers inside and around houses in Gede Settlement.

A. simpsoni.—Larvae from the empty shells of *Achatina* sp. (giant forest snail) (Taveta; Homer).

A. pembaensis.—Larvae common in the burrows (5–6 cm. in diameter) of the crab, *Sesarma eulimene*, in *Avicennia* forest; not taken in the smaller burrows (2–3 cm. diameter) of the crab, *Gelasima annulipes* (Latr.), which are mainly distributed on the forest edges and on open sand (Gede; Mida Creek).

Eretmapodites spp.—Early-instar larvae of the *E. oedipodius* group from riverside pools (Gede; River Sabaki). *E. chrysogaster* group, *E. quinquevittatus* and *E. sylvestris* ssp. *conchobius* identified from shells of *Achatina* sp. (Taveta; Homer).

Culex decens.—Larvae in a disused well; not taken in those in use (Gede).

Culex sp. indet.—In side pools of river (Gede; River Sabaki).

Tree holes.

The results of breeding up larval collections from tree holes may be summarised by species and some tentative comparisons of environments may be made.

GEDE.

Aëdes fulgens.—Common in *Trachylobium* forest; abundant in *Brachystegia* forest (♂♂, ♀ bred out).

A. metallicus.—Common in *Brachylaena* forest (♂♂ bred out); few in *Avicennia* forest.

A. soleatus.—Few in *Trachylobium* forest.

A. heischi.—Common in *Trachylobium* forest (♂♂, ♀♀ bred out) and *Adansonia* bush; occasional in *Brachystegia* and *Brachylaena* forests (♂♂, ♀♀ bred out).

A. haworthi and *A. ngong.*—Common in *Trachylobium* forest (♂♂, ♀♀ both species bred out).

A. furcifer and *A. taylori.*—Common in *Brachystegia* (one ♂ of each species bred out) and in *Brachylaena* forests and in *Adansonia* bush; a few in *Trachylobium* forest.

A. adersi.—Abundant in *Avicennia* forest.

A. michaelikati.—Common in *Brachystegia* (♂♂, ♀♀ bred out) and in *Brachylaena* (♂♂ bred out) forests and in *Adansonia* bush; occasional in *Trachylobium* forest.

Of all the environments, *Trachylobium* forest appears to be the richest in species; six of the eight species or groups recorded occurred there. Three species or groups—*A. heischi*, the *A. furcifer* group and *A. michaelikati*—were widespread, being present in four of the five environments studied, the exception in each case being the *Avicennia* forest. *A. fulgens* occurred in two environments. *A. haworthi* and *A. ngong* appeared to be confined to *Trachylobium* forest and *A. adersi* to the *Avicennia* forest.

It is of interest to note that some of the larvae from tree holes in the *Trachylobium* forest were found to be parasitised by larval nematode worms (*Agamomermis*) of the family Mermithidae. Species so affected were *A. soleatus*, *A. heischi* and *A. michaelikati*.

TAVETA.

Megarhinus brevipalpis.—Occasional in forest at Njoro (♂, ♀ bred out).
Aëdes fulgens.—Occasional at Homer and Mahou (♂ bred out).
A. ingrami.—Occasional at Njoro and Homer (♂♂, ♀♀ bred out).
A. aegypti.—Occasional at Njoro (♂♂ bred out).
A. metallicus.—Occasional at Njoro, Homer and Mahou (♂, ♀♀ bred out).
A. soleatus.—Common at Njoro (♂ bred out) and Homer (♂♂, ♀♀ bred out); abundant at Mahou (♂♂, ♀♀ bred out).
A. heischi.—Common at Njoro (♂♂, ♀♀ bred out) and at Homer (♂♂, ♀♀ bred out).
A. haworthi group.—Occasional at Njoro and Homer (♀ bred out).
A. taylori.—Abundant at Homer (♂, ♀♀ bred out); occasional at Njoro and Mahou.
A. michaelikati.—Occasional at Homer.
Eretmapodites chrysogaster group.—Occasional at Njoro.
Culex horridus.—Common at Njoro (♂ bred out); occasional at Homer.
C. nebulosus.—Common at Njoro (♂♂, ♀♀ bred out).

The bush locality (Mahou) appeared poorer in species than either of the forest ones but the bush sample was comparatively smaller. *A. aegypti* was not confined to tree holes close to huts.

Leaf axils.

Banana and pineapple plants were examined at Gede. No water-filled banana axils were discovered. Three water-filled axils, none with larvae, were found among 100 pineapple plants examined but these plants were watered artificially.

Water-retaining axils occurred at Taveta in seven kinds of cultivated plant but in one, colocasia, the axils had been filled with mud by a recent river flood, and so could not be satisfactorily searched. The results of examining standard samples of 50 axils in each of the other six were:—

English name	Kitaveta name	Percentage:—	
		With water	With larvae
Dragon tree (Dracaena) ..	Isal	80	46
Banana ..	Kisukari	50	14
,, ...	Ikojozi	40	14
,, ...	Ijiu	34	6
,, ...	Tarasa	10	2
,, ...	Tendera	6	0

Of 62 larvae identified, all were *A. simpsoni* except for four of the *E. chrysogaster* group; four adult *A. simpsoni* were bred out. Although Dracaena (*D. fragrans*) heads the list above as a breeding place of *A. simpsoni* it was much less abundant than bananas; it is considered that the main source of *A. simpsoni* at Taveta is banana plants, particularly of the varieties called kisukari and ikojozi in the Kitaveta language.

Oviposition pots.

GEDE.

A total of 378 pot-nights was recorded, of which 336 were exposures of bamboo pots and 42 of glass jars. The totals in the various environments were:— *Trachylobium* forest, 132; *Brachystegia* forest, 54; *Brachylaena* forest, 60; *Avicennia* forest, 72; *Adansonia* bush, 60. Two young larvae of the subgenus

Stegomyia, perhaps of *A. soleatus*, which occurred in one bamboo pot in *Trachylobium* forest, were the only indication of the presence of ovipositing mosquitos. The occurrence took place only about half a mile from an area in which the local African field entomological assistant carried out throughout the year a programme of filling tree holes with water and breeding out the resulting larvae; it is, therefore, open to the suspicion of having been caused by an escape from this artificial focus of breeding. However, the water in the pots often became foul and perhaps in this condition is not very attractive to ovipositing mosquitos of the subgenus *Stegomyia* (see below under Taveta).

TAVETA.

A total of 612 pot-nights was recorded for the forest localities Njoro and Homer, the pots being exposed near the ground and at about 18 m. Of these, 500 were exposures of bamboo pots and 112 of glass jars. *C. nebulosus* was overwhelmingly the commonest larva found at both localities and levels. Only at Njoro did other species occur—a few *Toxorhynchites* sp. at 18 m., a few *A.* (*Stegomyia*) sp. at both levels, and *E. chrysogaster* fairly commonly near the ground. Most of the *Stegomyia* larvae were immature and only *A. soleatus* was definitely identified (at 18 m.).

As at Gede, the water in many of the pots became turbid and ill-smelling and the incidence of such conditions in a marked degree may be compared with the type of pot involved. Of newly cut bamboos, 27 out of 32, of old bamboos, 3 out of 14, and of glass jars, none out of 11, became foul. Foulness of the water appears more likely to develop in newly cut bamboos than in old bamboos in which the internal coating of pith has rotted away previously, or in glass jars. There was little difference between the pots with markedly foul water and the others as far as the general incidence of larvae was concerned; 14 of the 30 with foul water contained larvae, 13 of the 27 others. Such water conditions are obviously attractive to females of *Culex nebulosus* as oviposition sites but are probably much less so to species of the subgenus *Stegomyia* whose larvae are usually associated with clear tea-coloured waters.

Discussion.

The reporting of the results of these two studies offers an opportunity to consider briefly also the general epidemiology of yellow fever in Kenya.

From the transience of the typical peripheral blood infection in the monkeys considered to be the main wild vertebrate hosts in tropical rain-forest it has been deduced that the location of survival of virus during periods when active cyclical transmission is in abeyance is most likely to be in the invertebrate host, *viz.*, in the mosquito, *Aëdes africanus*. The possibility of transovarial transmission of yellow fever virus from a mosquito to its progeny has been adequately studied in the case of *A. aegypti* (Davis & Shannon, 1930) and *A. africanus* (Gillett & others, 1950) but in neither was such transmission effected. Such findings, in two mosquito species known to be highly efficient vectors of virus both in the laboratory and the field, may be taken to indicate that inability to transmit virus to a succeeding generation is probably general among mosquitos. Thus persistence of yellow fever virus in an area does not seem possible except in the continual presence of adult mosquitos of a vector species, some of them acting as virus reservoirs. In Bwamba, Uganda, as an example of tropical rain-forest, this condition is fulfilled; *A. africanus* occurs as an adult even during the drier weather (Haddow, Gillett & Highton, 1947; Lumsden, 1952).

Although many mosquito species have been found capable of transmitting yellow fever virus by bite in the laboratory, only three have been incriminated in the field in Africa; these are *A. aegypti* (Beeuwkes & Hayne, 1931; Taylor, 1951), *A. simpsoni* (Mahaffy & others, 1942) and *A. africanus* (Smithburn, Haddow &

Lumsden, 1949). Mattingly (1952) has summarised the African locality records for these species of mosquito and his data for Kenya, largely derived from the work of Mrs. E. C. C. van Someren, may be briefly reviewed. *A. aegypti* has been recorded as high as 7,500 ft.; it is probably distributed throughout Kenya as a domestic species at altitudes below this level. It should be noted that it is not necessarily purely a domestic species; its larva has been recorded in tree holes in Mombasa (Wiseman & others, 1939) and at Taveta in the present work. *A. simpsoni* probably occurs as high as 6,000 ft.; it appears to be limited to areas receiving an annual rainfall in excess of 20 in., but in Kenya the only considerable area so excluded is a strip parallel to the coast between the coastal area and the highlands. Its distribution within the area possible is likely to be largely determined by the prevalence of plants offering leaf axils suitable for its breeding. Gillett (1951) has adduced evidence to show that *A. simpsoni* in some parts of Uganda does not bite man; this phenomenon may explain the low level of immunity which may exist in man alongside high levels of immunity in forest monkeys in some parts of Uganda. However, *A. simpsoni* is known to bite man in at least some parts of Kenya, *e.g.*, the Kerio Valley (Heisch, 1950) and Taveta (present work). With regard to *A. africanus*, Mattingly states that " its distribution is very closely and completely defined by the 40-in. isohyet except to the east of Lake Victoria where there is a complete altitudinal barrier ". Thus, of the areas of Kenya which annually receive more than 40 in. of rain—the region west of the Rift Valley, the coast as far north as about Lamu, and the vicinities of the great mountains—he considers that *A. africanus* has been excluded from all but part of the first by the barrier of the East African Highlands. The present record from Taveta, east of the Highlands, is probably to be regarded, as Mattingly regards the Abyssinian, Nyasaland and Mozambique records, as a relict population surviving in a special environment. But, if so, an originally continuous population south of the Highlands as well as to its north must be inferred and *A. africanus* may well be found to exist on the East African coast further to the south in areas which have not yet been adequately searched. The present work indicates that the population of *A. africanus* in Taveta differs in behaviour from the population of the main area of distribution.

The studies of Bailey (1947) and the present work have shown that mosquitos capable of transmitting yellow fever virus, at least in the laboratory, occur in the Gede area; these are *A. aegypti*, *A. simpsoni*, *A. metallicus* and *A. taylori*. So also at Taveta, proven vectors occur in *A. aegypti*, *A. simpsoni*, *A. metallicus* and *A. africanus*. Both areas are subject to a marked dry season, sometimes three consecutive months being quite without rain, and, in both, yellow fever virus is known to have occurred (Haddow, 1952).

At Gede an opportunity was available to assess the level to which the adult populations of probable vector mosquitos were reduced in the dry season. Tree holes were common in all the natural environments investigated and mosquito larvae could readily be obtained from them by filling them artificially with water. However, despite intensive searches, none was found naturally water-filled so that it may be concluded that mosquito breeding in tree holes is practically at a standstill towards the end of the dry season.

The only plant axils likely to retain water were found in cultivated banana and pineapple; none was found naturally water-filled but in this case the searches were less exhaustive and should be amplified by the results of other workers. Teesdale (1941), working in Mombasa, records that *A. simpsoni* commonly, and *A. aegypti* and *A. metallicus* sometimes, breed in the axils of both banana and pineapple plants. However, he states that in " some hundreds " of banana plants examined after 43 days of drought there was never any water in the upper leaf axils where water and larvae were commonly to be found in wet weather; although he records that water persisted in many plants near their bases, mosquito breeding there appears to have been rare and larvae were only found on one occasion. Similarly, no water or larvae were found in the axils of "a large number" of pineapple plants examined after a period of three months during which "no appreciable rainfall" had occurred. Even in the comparatively uniform climate of Bwamba, Uganda, Haddow (1948) records that the proportions of axils of colocasia plants (*Xanthosoma sagittifolium*) which contained water and mosquito larvae were severely reduced in the drier weather. Although he considered that this effect was due largely to differences in the state of the plants, he points out that the growth of the plants is affected by the rainfall and states that for a short period all axils dried out completely. It would appear that breeding by mosquitos in plant axils also is liable to be severely reduced in long-continued dry weather. Continued breeding of a vector species in the dry season at Gede was demonstrated, however, in the finding of larvae of *A. aegypti* in domestic containers. In the domestic environment the attack of this species must be mainly on man, at least as far as primates are concerned. The high level of artificially-induced immunity in man in the area renders the persistence of virus by a series of *A. aegypti*-man cycles very unlikely.

At Taveta it appears possible that breeding of some vector species could continue through the dry season. Tree holes and axils in the forest may be expected to dry out much more slowly than at Gede when rain ceases as the humidity in the forest is probably high at all seasons (the forest is abundantly supplied with ground water) and the main dry season falls at the coolest time of the year; both these factors will tend to slow down the rate of evaporation of water in tree holes and plant axils.

Although the foregoing indicates that the breeding of likely vector species at Gede is liable to be severely curtailed or even stopped completely (except in the case of *A. aegypti*, which is considered unimportant for other reasons, see above) the survival through a dry season of adults hatched before its onset must be considered. No adult mosquitos of species likely to be vectors occurred in extensive catches, both on stationary and moving human baits in any of the natural environments investigated. A considerable sample of water-filled pots put out in the several environments failed to show any evidence that oviposition had taken place in them except in one case in which the occurrence is open to some suspicion of having been artificially caused. Too great weight should not, however, be given to the largely negative results of work with oviposition pots, as comparison with the results of similar work carried out at Taveta, in a wet period, shows that bamboo pots are rather unsuitable. There is no doubt that suitable conditions for oviposition and the subsequent development of mosquito larvae do arise in pots of this kind (*vide* Garnham, Harper & Highton, 1946) but in using them for the critical demonstration of adult mosquitos during periods of drought it is necessary to remove any doubt that larvae subsequently obtained from them could be derived from drought-resistant eggs left in the pots from previous use. As *Aëdes* females tend to lay their eggs in sheltered positions such as cracks and crevices (Marshall, 1938), simple washing out of the pots cannot be accepted as a sufficient precaution. It is well known that mature drought-resistant eggs do not necessarily all hatch on the first flooding with water (various authors quoted in Marshall, 1938). It appears, therefore, that the finding of larvae in water-filled pots put out in forest or other environments during a period of drought cannot be accepted as incontrovertible evidence of the presence of adult mosquitos unless it is specifically stated that the pots have been previously sterilised. In the present work at Gede and Taveta the pots were filled before use with boiling water, which was allowed to remain in them for about ten minutes, until the pot was thoroughly heated throughout. After this treatment it was possible to be confident that no living eggs remained, but water subsequently placed in the pots tended to become turbid and evil-smelling, perhaps on account of alterations to the normal bacterial flora caused by the treatment. Such water was shown by experience at Taveta to be highly attractive to *Culex nebulosus* as a place of oviposition but the rarity of other tree-hole-breeding species in comparison indicates that it is less attractive to them and the scarcity of larvae at Gede may be due to this fact as much as to the lack of adults to oviposit. It is considered that, for critical work of this kind, it will be necessary to use easily sterilised pots, probably of earthenware, and to add to them water of known attractiveness, freed from eggs, perhaps filtered natural tree-hole water. Robinson (1950) has recorded the results of similar work with oviposition pots in Northern Rhodesia. While his records of larval occurrences in dry weather are open to doubt as the pots were simply washed out, he mentions the more significant fact that adult females of *A. africanus* were taken in sticky traps attached to the mouths of the pots. That these adults were hatched from breeding within the pots seems to be precluded by the frequency (twice weekly) with which the pots were washed out and examined. However, he refers to the surviving adult *Aëdes* population during the dry season as " skeleton ".

There remains the possibility that the surviving adult population is in fact a large one, simply rendered difficult of detection by reason of inactivity. If this is so, it would be expected that, on conditions again becoming favourable, large numbers of old females would appear as biting adults. However, Lumsden (1952) has paid some attention to detecting an effect of this kind in Bwamba, Uganda, without finding any evidence of its existence.

Thus no evidence has yet been produced to show that more than a very few adult mosquitos of species likely to be vectors are present towards the end of periods of prolonged drought. Such a reduction in the population of adult mosquitos appears likely, assuming no other mechanism, to render the persistence of yellow fever virus in such areas at least precarious. The number of virus-infected mosquitos may apparently be a very small proportion of the population; Haddow, Smithburn & others (1948) record that over 6,000 *A. africanus* collected in forest in various parts of Uganda were inoculated into susceptible monkeys before the presence of yellow fever virus was demonstrated. If this conclusion is accepted, the main possibilities remaining are that virus does in fact die out in such areas yearly, or at least in the more severe dry seasons, or that transmission is maintained during long continued dry seasons by other species of mosquito, or by a cycle involving some other arthropod.

Lumsden & Buxton (1951) considered the first possibility a likely one for West Nile District, Uganda, but this area is in fairly close relation to localities of evenly-distributed rainfall in which tropical forest is developed, and they considered that the periodic re-introduction of virus from such areas by the carriage of infected mosquitos over long distances at high levels by wind was a distinct possibility. In Kenya, however, particularly in coastal localities such as Gede, the distances involved in such an explanation are much greater and it is correspondingly less attractive.

The three vectors of yellow fever virus so far shown to be important in the field in Africa all belong to the small-container breeding group and particular attention has always been devoted in yellow fever studies to mosquito species using this type of breeding place. Nevertheless, as is shown by laboratory studies, capability to transmit yellow fever virus by bite is not confined to this group of mosquitos. Probably many species of mosquitos have the capability, at least it has been shown in the laboratory for representatives of three genera of mosquitos and of three subgenera within the genus *Aëdes*. Examples are *Taeniorhynchus africanus*, *Aëdes* (*Stegomyia*) *aegypti* var. *queenslandensis* (Theo.), *A. metallicus*, *A. africanus*, *A. luteocephalus* (Newst.) and *A. vittatus* (Big.), *A.* (*Aëdimorphus*) *stokesi* Evans, *A.* (*Diceromyia*) *taylori*, *Culex thalassius* Theo. and *C. pipiens fatigans* (Bauer, 1928; Philip, 1929; Kerr, 1932; Davis, 1933; Lewis, Hughes & Mahaffy, 1942). Some of these species have been suspected on epidemiological grounds but virus has been isolated in Africa only from *A. aegypti*, *A. simpsoni* and *A. africanus* (see above). At least one of the species proved capable of effecting transmission in the laboratory by bite has appeared to be of little or no importance in the field; during the period and in the area of active yellow fever transmission in the forest in Bwamba in 1948, yellow fever virus was not demonstrated in 2,428 *Taeniorhynchus africanus* and *T. uniformis* (of which the former species was much the more plentiful) by inoculation into susceptible monkeys (*Macaca mulatta*), while it was repeatedly shown in the same catches and by the same methods in a total of 2,040 *Aëdes africanus* (Smithburn, Haddow & Lumsden, 1949). However, attention has been drawn to *Culex poicilipes* and *C. univittatus* in the West Nile District, Uganda, as being species whose biting-cycles and vertical distributions indicate that their main attack may be on monkeys and as being species which are present as biting adults at the height of the dry season as they breed in relict pools of water (Lumsden & Buxton, 1951; Lumsden & van Someren, 1953). The present study shows that *A. fryeri* and *A. pembaensis*, which breed in sea water, are present as biting adults in the dry season in the Gede area and could conceivably be responsible for continuing cycles of virus transmission at this time. Nothing is yet known, however, of the efficiency of these latter species as virus vectors and they could only be important in this manner in coastal areas as they do not penetrate far inland; 224 were taken in a total of five days' 24-hour catching in and near mangrove forest, only six in nine days' similar work at forest localities more inland but still not more than 7 miles from the sea. It is probable that in most areas in which yellow fever virus occurs and which experience a prolonged dry season, some mosquito species might be found to fulfil the basic condition of being present as a biting adult during the dry season but the explanation of virus survival on such grounds seems likely to involve many different mosquito species. Previous experience indicates that the mosquito species important in the transmission of yellow fever virus in the field are few, despite the considerable numbers shown capable of acting as vectors in the laboratory.

Haddow (1952) has summarised the results of the yellow fever protection tests made on wild primates from Kenya. Although immunity to yellow fever did occur occasionally among monkeys it was significantly more common in a lemuroid, *Galago crassicaudatus*. A similar situation, involving, however, a different species of galago, *G. senegalensis*, appears to exist in Karamoja District, one of the drier parts of Uganda (Haddow, *loc. cit.*). Both species have been demonstrated to be satisfactory host-animals in the laboratory (Smithburn & Haddow, 1949; Bugher, 1951). It does not seem possible to explain the distribution of immunity to yellow fever in primates in Kenya by reference to any of the three proven field vectors, *A. aegypti*, *A. simpsoni* or *A. africanus*. Lumsden (in press) concluded from a critical study of protection tests that the introduction of yellow fever virus into man in Kenya is at the most a rare occurrence. Yet *A. aegypti* appears to be a widespread domestic mosquito; it was found to be common in houses even under the comparatively good living conditions of Gede Settlement.

Catches of biting mosquitos at human bait in forest localities at Taveta showed *A. simpsoni* to be abundant both at ground level and in the canopy. In a sample of 64 human sera from the same localities only four were found immune and at least three of these are open to the suspicion of being artificially caused, the result of vaccination with 17D vaccine (Lumsden, in press). Similarly, of a sample of 49 monkey sera, none was immune (Haddow, 1952). If it can be assumed that, at Taveta, *A. simpsoni* attacks monkeys as actively as it does man and that it is an efficient vector, then neither of these observations can be explained except by supposing that yellow fever virus has not yet been introduced into the system. Yet it has affected the galago population in the same localities (Haddow, 1952). Immunity to yellow fever has been demonstrated in wild primates (Haddow, 1952) in two places in which *A. africanus* has not been discovered despite careful search; these places are Gede (Bailey, 1947; and the present work) and the Langata Forest near Nairobi (Garnham, 1949). Further, although *A. africanus* occurs at Taveta, the monkey sample was uniformly non-immune though this may perhaps be adequately explained by the anomalous behaviour of *A. africanus* there. At Taveta only one of the 19 specimens collected was taken between sunset and sunrise and the species was only slightly more abundant at the 18 m. level than it was on the ground. In Uganda and in West Africa it has been accepted as a species biting mainly at the upper forest levels and in the hour following sunset (Haddow, Gillett & Highton, 1947; Mattingly, 1949; Lumsden, 1952), which habits have been considered to indicate that it largely attacks monkeys, as at this time and place the monkeys are quiescent in their sleeping trees (Haddow, Smithburn & others, 1947; Lumsden, 1951*b*) and are likely to offer suitable conditions for mosquitos to bite. The behaviour of the species at Taveta suggests that its attack there may be mainly on some animal other than monkeys. However, the species may not be widespread in the Taveta forests; it occurred in the very damp conditions near the Njoro springs, not in the drier type of forests at Homer.

Enough evidence has now been presented to indicate that the mode of transmission and persistence of yellow fever virus in Kenya, and in the drier parts of Uganda, is likely to differ from the mechanism which has been advanced to explain the epidemiology of the disease in areas of tropical rain-forest and which has, in those areas, agreed satisfactorily with all the evidence brought forward. Detailed studies of the biology of galagos are now necessary to orientate future research on the arthropods responsible for transmission of yellow fever virus among them, which aspect at the moment is only a matter for conjecture.

The assessment of the frequency with which yellow fever virus reaches the human population in Kenya is rendered difficult, if not impossible, by the common occurrence of artificially-produced immunity consequent on the recent free distribution of 17D yellow fever vaccine among the African population. This matter has been studied by Lumsden (in press) who found that, for Africans, the recorded vaccinations amounted to over 7 per cent. of the total population. He cites evidence (Smithburn & Mahaffy, 1945) to show that this vaccine produced a high proportion (about 90%) of demonstrably immune individuals among those inoculated and to show that such immunity may be recognised up to nine years after vaccination (Dick & Gee, 1952). The same paper presents the result of protection tests made on the sera of samples of residents in the Gede and Taveta areas. The donors of sera were subjected to a close interrogation and after elimination of those individuals who, on their statements, had clearly been exposed to the possibility of vaccination, only three immunes out of the total of 27 discovered in the Gede area and one out of the four at Taveta, remained. Even in these cases it was considered that, in view of the extent of African population movement and the difficulty of confirming statements made, even these were open to the suspicion of having been artificially caused. However, some certain evidence exists that yellow fever virus may reach man in Kenya by natural means. This is afforded by the immune individual discovered in Kisii in 1933–4 before vaccination against yellow fever had become available in East Africa and by two fatal cases (for details see Lumsden, in press). The demonstration of past yellow fever infection in wild mammals on the Kenya coast indicates in all probability that the presence of the virus there is an affair of long standing and not merely a recent introduction, associated with the modern facility of travel, from more western parts of Africa. If virus has in the past reached the human population in coastal districts of Kenya it is difficult, in view of the presence of *A. aegypti*, to understand the lack of records of epidemics in these areas and in Asiatic ports; Furlong (1947) has shown that breeding of *A. aegypti* may take place in modern dhows engaged in the traffic between the East African littoral and Asia and this traffic is apparently one of considerable antiquity (for discussion of this matter see Hornell, 1934). It is considered that the balance of evidence indicates that the introduction of yellow fever virus into the human population in Kenya has been only very rare, as, also, it has been among monkeys. From the prevalence of immunity to yellow fever among galagos and its rarity among man and monkeys despite the presence of mechanisms which would be expected to be efficient in disseminating virus among them it may be deduced that the galago cycle is likely to be entirely separate and self-contained. Taveta affords an example of a situation which apparently only awaits the transference of virus from the galago cycle into the man-monkey-*A. africanus*-*A. simpsoni* complex for widespread transmission therein to take place.

Summary.

The theoretical objections to the explanation of the persistence of yellow fever virus in areas subject to a prolonged dry season by cycles involving only mosquitos and wild primates are discussed in relation to the results of field surveys in areas of this type in Kenya. The localities studied were Gede, on the coast about 65 miles north of Mombasa, and Taveta, near Mount Kilimanjaro.

The topography, climate, vegetation and human population of the areas are briefly described.

Gede was visited towards the end of the dry season, Taveta during the main wet season. Thus most of the data relating to conditions during the dry season are derived from Gede, the results from Taveta being used mainly for comparative purposes. The work included 24-hour baited catches at two levels, moving catches, and larval collections in all the main typical environments.

All the species of biting arthropod encountered at each locality are recorded; in each case most were mosquitos.

At Gede the only mosquitos which were abundant as biting adults were species which breed in sea water, *Aëdes fryeri* (Theo.) and *A. pembaensis* (Theo.), and they were practically confined to the close vicinity of their breeding places. The vertical distributions and biting-cycles of these species are defined.

At Gede, mosquito larvae could readily be obtained by filling tree holes artificially with water but no naturally water-filled tree holes were discovered by intensive searches in all the natural environments present in the area. Nor were any water-containing leaf axils discovered.

Attempts to demonstrate the presence of adult mosquitos of the small-container breeding habit in natural environments during the dry season by means of oviposition pots are reported for Gede and are compared with the results at Taveta. The fallacies of, and precautions necessary in, such work are discussed.

A. (*S.*) *simpsoni* (Theo.), a proven field vector of yellow fever virus to man in Uganda, was found abundantly biting man at Taveta and this occurrence is discussed in relation to the at most very low proportion of immune humans discovered there.

A. (*S.*) *africanus* (Theo.), a proven field vector of yellow fever virus among monkeys in Uganda, was found at Taveta but its behaviour differed considerably from what is considered characteristic of the species in Uganda and West Africa. Its occurrence and behaviour are discussed in relation to the demonstrated lack of immunity to yellow fever among wild monkeys at Taveta.

It is concluded that the present work, and other work cited, have so far failed to show that mosquitos of the small-container breeding habit, among which

yellow fever virus vectors are usually to be sought, are present in more than very small numbers as adults after a prolonged drought. This is considered to render precarious the persistence of virus in such an area by cycles involving only these mosquitos and wild mammals. Other possibilities concerning mosquitos are discussed.

Attention is drawn to the recent finding (Haddow, 1952) that galagos are apparently more involved in the epidemiology of sylvan yellow fever in Kenya than are monkeys and it is concluded that a detailed study of the biology and ectoparasites of these animals is a prerequisite for further advance.

Acknowledgements.

I am deeply indebted for assistance to many officers of the Kenya Administration and Technical Services but particularly to the Director of Medical Services (Dr. T. Farnworth Anderson), the Staff of the Medical Research Laboratory in Nairobi (Dr. R. B. Heisch, Dr. S. Avery Jones, Mrs. E. C. C. van Someren and Mr. A. E. C. Harvey) and to workers in the areas studied (Dr. W. L. Barton, Kilifi, and Mr. C. Teesdale, Mombasa). Various authorities have freely given their assistance in the identification of material; they were Professor J. J. C. Buckley (Nematoda), Dr. W. E. China (Hemiptera), Dr. F. van Emden (Muscidae), Dr. I. Gordon (Crustacea), Mr. P. F. Mattingly (Culicidae), Mr. H. Oldroyd (Tabanidae), Mr. C. G. Radford (Mites), and Dr. F. Zumpt (Ixodoidea). For climatic data we are indebted to the East African Meteorological Department. Dr. A. J. Haddow collected the mammal ectoparasite material (ticks and mites) and provided the data of the night catch near the Tana river. Mr. J. M. Ellice rendered valuable assistance during the course of the surveys and in the subsequent examination of material. The African Field Staff of the Institute gave very great service in the field, often under very trying climatic conditions.

References.

Bailey, K. P. (1947). A preliminary note on the sylvan mosquitos of Gede.—E. Afr. med. J., **24**, pp. 38–41.

Bauer, J. H. (1928). The transmission of yellow fever by mosquitoes other than *Aëdes aegypti*.—Amer. J. trop. Med., **8**, pp. 261–282. (Abstr. in Trop. Dis. Bull., **25**, p. 848.)

Beeuwkes, H. & Hayne, T. B. (1931). An experimental demonstration of the infectivity with yellow fever virus of *Aëdes aegypti* captured in an African town.—Trans. R. Soc. trop. Med. Hyg., **25**, pp. 107–110.

Bugher, J. C. (1951). The mammalian host in yellow fever.—*In* Strode, G. K. *Ed.* Yellow fever, pp. 299–384. New York, McGraw-Hill.

Dale, I. R. (1939). The woody vegetation of the coast province of Kenya.—Inst. Pap. For. Inst. Oxf., no. 18, 28 pp.

Davis, N. C. (1933). Transmission of yellow fever virus by *Culex fatigans* Wiedemann.—Ann. ent. Soc. Amer., **26**, pp. 491–495.

Davis, N. C. & Shannon, R. C. (1930). The location of yellow fever virus in infected mosquitoes and the possibility of hereditary transmission.—Amer. J. Hyg., **11**, pp. 335–344.

Dick, G. W. A. & Gee, F. L. (1952). Immunity to yellow fever nine years after vaccination with 17D vaccine.—Trans. R. Soc. trop. Med. Hyg., **46**, pp. 449–458.

Furlong, M. (1947). *Aëdes* control at Lamu.—E. Afr. med. J., **24**, pp. 36–38.

Garnham, P. C. C. (1949). Acrodendrophilic mosquitos of the Langata Forest, Kenya.—Bull. ent. Res., **39**, pp. 489–490.

Garnham, P. C. C., Harper, J. O. & Highton, R. B. (1946). The mosquitos of the Kaimosi Forest, Kenya Colony, with special reference to yellow fever.—Bull. ent. Res., **36**, pp. 473–496.

Gillett, J. D. (1951). The habits of the mosquito *Aëdes* (*Stegomyia*) *simpsoni* Theobald in relation to the epidemiology of yellow fever in Uganda.—Ann. trop. Med. Parasit., **45**, pp. 110–121.

Gillett, J. D., Ross, R. W., Dick, G. W. A., Haddow, A. J. & Hewitt, L. E. (1950). Experiments to test the possibility of transovarial transmission of yellow fever virus in the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald.—Ann. trop. Med. Parasit., **44**, pp. 342–350.

Gillman. C. (1949). A vegetation-types map of Tanganyika Territory.—Geogr. Rev., **39**, pp. 7–37, 1 pl.

Haddow, A. J. (1945). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—Bull. ent. Res., **36**, pp. 33–73.

Haddow, A. J. (1948). The mosquitoes of Bwamba County, Uganda. VI. Mosquito breeding in plant axils.—Bull. ent. Res., **39**, pp. 185–212.

Haddow, A. J. (1950). A note on the occurrence of *Aëdes* (*Stegomyia*) *simpsoni* Theobald in the canopy of rain-forest in Bwamba County, Uganda.—Ann. trop. Med. Parasit., **44**, pp. 238–241.

Haddow, A. J. (1952). A review of the results of yellow fever protection-tests on the sera of primates from Kenya.—Ann. trop. Med. Parasit., **46**, pp. 135–143.

Haddow, A. J., Gillett, J. D. & Highton, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate.—Bull. ent. Res., **37**, pp. 301–330.

Haddow, A. J., Smithburn, K. C., Dick, G. W. A., Kitchen, S. F. & Lumsden, W. H. R. (1948). Implication of the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald in the forest cycle of yellow fever in Uganda.—Ann. trop. Med. Parasit., **42**, pp. 218–223.

Haddow, A. J., Smithburn, K. C., Mahaffy, A. F. & Bugher, J. C. (1947). Monkeys in relation to yellow fever in Bwamba County, Uganda.—Trans. R. Soc. trop. Med. Hyg., **40**, pp. 677–700.

Heisch, R. B. (1950). Survey of the Kerio Valley.—E. Afr. med. J., **27**, pp. 233–242.

Hopkins, G. H. E. (1952). Mosquitoes of the Ethiopian Region. I. Larval bionomics of mosquitoes and taxonomy of Culicine larvae.—2nd edn., 355 pp. London, Brit. Mus. (Nat. Hist.).

Hornell, J. (1934). Indonesian influence on East African culture.—J. R. anthrop. Inst., **64**, pp. 305–332.

Kauntze, W. H. & Symes, C. B. (1933). Anophelines and malaria at Taveta.—Rec. med. Res. Lab. Kenya, no. 5, 26 pp.

Kerr, J. A. (1932). Studies on the transmission of experimental yellow fever by *Culex thalassius* and *Mansonia uniformis*.—Ann. trop. Med. Parasit., **26**, pp. 119–127.

Kirkpatrick, T. W. (1925). The mosquitoes of Egypt.—224 pp. Cairo, Egypt. Govt. Anti-Malar. Comm.

Lewis, D. J., Hughes, T. P. & Mahaffy, A. F. (1942). Experimental transmission of yellow fever by three common species of mosquitoes from the Anglo-Egyptian Sudan.—Ann. trop. Med. Parasit., **36,** pp. 34–38.

Lumsden, W. H. R. (1951*a*). Probable insect vectors of yellow fever virus, from monkey to man, in Bwamba County, Uganda.—Bull. ent. Res., **42,** pp. 317–330.

Lumsden, W. H. R. (1951*b*). The night-resting habits of monkeys in a small area on the edge of the Semliki Forest, Uganda. A study in relation to the epidemiology of sylvan yellow fever.—J. Anim. Ecol., **20,** pp. 11–30.

Lumsden, W. H. R. (1952). The crepuscular biting activity of insects in the forest canopy in Bwamba, Uganda. A study in relation to the sylvan epidemiology of yellow fever.—Bull. ent. Res., **42,** pp. 721–760.

Lumsden, W. H. R. & Buxton, A. P. (1951). A study of the epidemiology of yellow fever in West Nile District, Uganda.—Trans. R. Soc. trop. Med. Hyg., **45,** pp. 53–78.

Lumsden, W. H. R. & van Someren, E. C. C. (1953). Records of *Culex* species (Diptera: Culicidae) from West Nile District, Uganda, with notes on their behaviour.—Proc. R. ent. Soc. Lond., (B) **22,** pp. 19–22.

Mahaffy, A. F., Smithburn, K. C., Jacobs, H. R. & Gillett, J. D. (1942). Yellow fever in western Uganda.—Trans. R. Soc. trop. Med. Hyg., **36,** pp. 9–20.

Marshall, J. F. (1938). The British mosquitoes.—341 pp. London, Brit. Mus. (Nat. Hist.).

Mattingly, P. F. (1949). Studies on West African forest mosquitos. Part I. The seasonal distribution, biting cycle and vertical distribution of four of the principal species.—Bull. ent. Res., **40,** pp. 149–168.

Mattingly, P. F. (1952). The sub-genus *Stegomyia* (Diptera: Culicidae) in the Ethiopian Region. (Part I.)—Bull. Brit. Mus. (nat. Hist.), Ent., **2,** pp. 233–304.

Milne, G. (1936). A provisional soil map of East Africa (Kenya, Uganda, Tanganyika and Zanzibar) . . .—Amani, E. Afr. agric. Res. Sta.

Murray, Sir J. (1913). The ocean.—256 pp. London, Thornton Butterworth.

Philip, C. B. (1929). Preliminary report of further tests with yellow fever transmission by mosquitoes other than *Aëdes aegypti*.—Amer. J. trop. Med., **9,** pp. 267–269. (Abstr. in Trop. Dis. Bull., **26,** p. 1005.)

Robinson, G. G. (1950). A note on mosquitoes and yellow fever in Northern Rhodesia.—E. Afr. med. J., **27,** pp. 284–288.

Smit, F. G. A. M. (1952). Descriptions of two new fleas, with a redescription of the genus *Chimaeropsylla* Rothschild, 1911.—Ann. Mag. nat. Hist., (12) **5,** pp. 844–856.

Smithburn, K. C. & Haddow, A. J. (1949). The susceptibility of African wild animals to yellow fever.—Amer. J. trop. Med., **29,** pp. 389–423.

Smithburn, K. C., Haddow, A. J. & Lumsden, W. H. R. (1949). An outbreak of sylvan yellow fever in Uganda with *Aëdes* (*Stegomyia*) *africanus* Theobald as principal vector and insect host of the virus.—Ann. trop. Med. Parasit., **43,** pp. 74–89.

Smithburn, K. C. & Mahaffy, A. F. (1945). Immunization against yellow fever . . .—Amer. J. trop. Med., **25,** pp. 217–223.

Taylor, R. M. (1951). Epidemiology.—*In* Strode, G. K. *Ed.* Yellow fever, pp. 427–538. New York, McGraw-Hill.

Teesdale, C. (1941). Pineapple and banana plants as sources of *Aëdes* mosquitoes.—E. Afr. med. J., **18,** pp. 260–267.

Wiseman, R. H., Symes, C. B., McMahon, J. C. & Teesdale, C. (1939). Report on a malaria survey of Mombasa.—60 pp. Nairobi, Govt. Printer.

ABNORMALITIES EXHIBITED BY MOSQUITO LARVAE COLLECTED IN TONGA.[1]

By Marshall Laird, D.Sc., Ph.D.[2]

A number of larval habitats of *Culex* (*Culex*) *annulirostris* Skuse were studied near Nuku'alofa, Tongatapu, during a brief visit on 26th October 1953. Subsequently, while permanent preparations were being made, two larvae were seen to be abnormal. These, a fourth-instar and what appeared to be an early third-instar, had been collected from a slightly brackish pool near Fanga Uta lagoon.

Fifteen other larvae (second to fourth instars) from the same pool were normal in every respect. The occurrence is thought worthy of record, as this is the first occasion on which such abnormalities have been observed in the course of 21 months' field work. Upwards of 10,000 larvae of *C. annulirostris* alone, from many parts of the Pacific, have been examined during this period.

Material.

The fourth-instar larva in question exhibits duplication of the left clypeal spine and its basal tubercle (fig. 1 (a)). Each of the resultant spines is little more than half the width of that on the other side of the preclypeus, this one (fig. 1 (b)) being perfectly normal. The basal tubercles of the twinned spines are closely adjacent and are much smaller than usual. One further abnormality is evident in this larva, the lower eight hairs of the left antennal tuft each being bent at right angles a third of the way along the shaft.

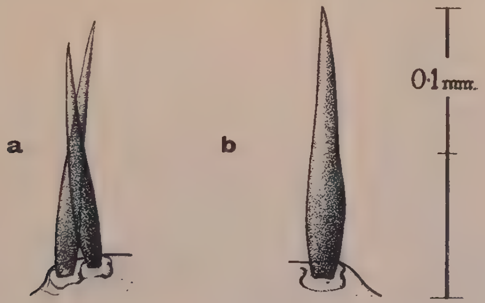


Fig. 1.—Duplicated (a) and normal (b) clypeal spines from the same fourth-instar larva of *Culex annulirostris* Skuse.

The abnormalities of the other larva are in the form of gross malformations. The siphon (fig. 2 (a)) is sharply curved in a ventro-lateral direction a little beyond its mid-point, and its distal portion is slightly twisted in a plane at right angles to that of the obvious curve. A normal siphon of *C. annulirostris* at an equivalent stage of development is illustrated in fig. 2 (b) the outline of portion of the siphon under consideration also being indicated at the same scale. As is shown in fig. 1 (a) the chitin of the abnormal siphon is thrown into irregular transverse folds and ridges in the area of maximum distortion. Both siphonal tracheae are somewhat malformed and are narrower than usual, but the pecten and ventro-lateral hair tufts are in the normal state.

---

[1] This study forms part of a project initiated by the Royal New Zealand Air Force and supported by a grant from the N.Z. Department of Scientific and Industrial Research. Its publication is authorised by the Chief of Air Staff, RNZAF.

[2] Medical Branch, RNZAF.

Both antennae of the smaller larva are likewise grossly distorted (fig. 2 (c)), the proximal part of the shaft being twisted in two planes (normal condition illustrated in fig. 2 (d)). There is usually a sharp distinction between the pale

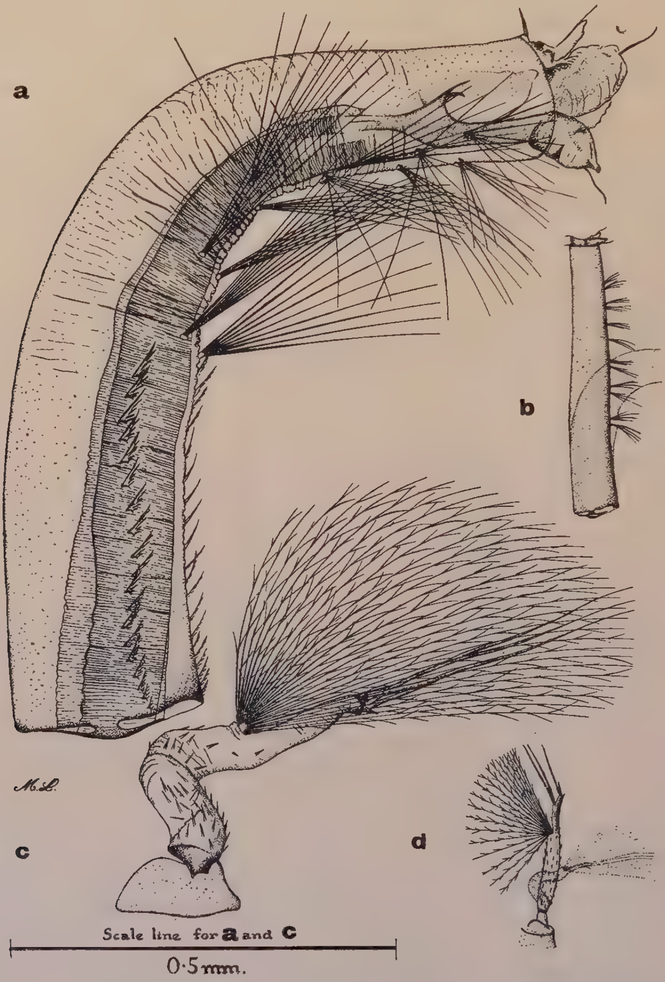


Fig. 2.—Malformations in an abnormal larva of *Culex annulirostris* Skuse, apparently in third instar.
(a) Malformed siphon (× 102).
(b) Normal appearance of siphon of third instar (× 26), with indication of a portion of the siphon illustrated in (a).
(c) Malformed antenna (× 102).
(d) Normal appearance of antenna of third instar (× 26), the figure superimposed on a dotted outline of the antenna illustrated in (c).

colour of the proximal two-thirds of the antennal shaft and the dark colour of the distal third, in larvae of *C. annulirostris*. Cooling (1924) pointed out that such coloration of the antennae is the rule among those Culicines in which the larva has a long siphon and the adult has a white-banded proboscis. Such a distinction is only barely evident in the right antenna (that figured) of the larva under consideration, the distal portion being almost as pale as the proximal portion, although the left antenna is normal in this respect.

Discussion.

Langeron (1928) noted duplications of various adjuncts of the cuticle in Anopheline and Culicine larvae in France, Corsica and North Africa. Duplicated hairs tended to remain appressed to the cuticle in hoops and circlets. The phenomenon was more commonly observed in Anopheline than in Culicine larvae, and in the latter only abdominal and thoracic hairs were affected. Langeron regarded this kind of abnormality as a precocious development anticipating a normal moult. J. Gaud (private communication, 1953) interpreted Langeron's "hoops" as the hairs of the new envelope seen through the old larval skin, the latter having persisted in an abnormal fashion.

Gaud & Laurent (1950) described a doubling of hairs (in North African *Anopheles* larvae) of a type more closely comparable with that under discussion. These authors found 28 instances of such an abnormality of the clypeal hairs in the course of an examination of 26,000 larvae representing six species. They also discovered two larvae exhibiting a doubling of the maxillary palp hair, and two having a frontal hair doubled. The duplication of hairs was seen in third and fourth instars only. While at first they had been inclined to regard the phenomenon as an example of teratology, Gaud & Laurent felt that this explanation, a plausible one had the abnormality been confined to a single group of hairs, was not supported by their later record of duplicated frontal and palp hairs. They also pointed out that if the affected larvae were indeed monsters, the phenomenon would be encountered at least as frequently, if not more so, among first and second instars. No larvae of either of these instars, although many were examined, were ever found to have doubled hairs. Thus, drawing attention to the fact that the hairs concerned are those at the vulnerable anterior end of the body, Gaud & Laurent interpreted the duplication under their notice as being due to the adventitious injury of the hair bud.

The duplication of a clypeal spine described for one of the larvae from Tonga would lend itself to explanation on the same grounds, particularly as each of the resultant elements is only about half the width of a normal spine, were it not for the unusual bending of some of the hairs of an antennal tuft in the specimen in question, and for the grossly malformed state of a second and smaller larva from the same pool. Of course, the malformations of the second larva, if seen alone, might be interpreted as due to injuries suffered at hatching or moulting. In any case, they might have been responsible for a decrease in the rate of development of the larva concerned, so causing it to seem younger than its age. Provided that one is prepared to invoke a high degree of coincidence, the hypothesis of adventitious injury is thus applicable to both instances of abnormality under discussion.

Recognising, however, that no other abnormalities were disclosed in the course of the examination of over 10,000 larvae of *C. annulirostris*, and that not only closely related individual mosquitos but even one and the same adult could have originated two broods in the pool concerned, the possibility that we are dealing with an instance of teratology cannot be disregarded.

A microscopic slide on which are mounted the larvae discussed herein has been deposited in the collection of the Dominion Museum, Wellington, New Zealand.

Summary.

The duplication of a clypeal spine and the bending of some of the hairs of an antennal tuft in a fourth-instar larva of *Culex* (*Culex*) *annulirostris* Skuse, and the gross malformation of the antennae and siphon of an apparently younger larva from the same pool, are described and discussed.

Acknowledgements.

Assistance in the collection of this material was rendered by my wife and by T. M. P. Kuli Helu of the Department of Health, Tonga.

References.

Cooling, L. E. [1924]. The larval stages and biology of the commoner species of Australian mosquitoes. . .—Serv. Publ. Dep. Hlth Aust. trop. Div., no. 8, 40 pp.

Gaud, J. & Laurent, J. (1950). Les soies doublées chez les larves d'*Anopheles*. —Ann. Parasit. hum. comp., **25**, pp. 480–484.

Langeron, M. (1928). Les larves anormales de moustiques, ou larves à collier et à cerceaux.—Ann. Parasit. hum. comp., **6**, pp. 273–283.

THE RELATIVE CONTROL VALUES OF DIFFERENT PERCENTAGE MORTALITIES.

By M. E. Solomon

E.M.N

Department of Scientific and Industrial Research,
Pest Infestation Laboratory, Slough, Bucks.

In treatments with insecticides a proportion of the pest population often survives and subsequently multiplies. The economic significance of this depends on various factors, including the power of increase of the pest, and the remaining time available for its increase. When stored products are fumigated, the significance of survivals depends largely on these two factors. Residues of fumigant have no lasting effect, and in most cases there are no predators or parasites whose removal might influence the course of events.

The rate of increase is influenced by the physical conditions. These are stabilised in varying degrees by the building and more particularly by the masses of stored materials when the pests are living within them, but gradients of temperature and moisture are common, and local heating sometimes develops. Another factor which may influence the rate of increase is population density, if this is very high or very low (Solomon, 1953). Whether or not it is likely to have much effect will depend on the species and the density levels involved. It is only when such effects of density and of variations in physical conditions can be ignored, or allowed for by calculation, that the following method can be applied. *The method consists in calculating the relative values of different percentage mortalities in terms of the times required by the reduced populations of pests to return to their former densities.*

If the growth of the population of a certain pest under the conditions of storage is exponential, and the rate of increase is x, so that a population of 1,000 increases to $1{,}000x$ after one week, and if the time in weeks to recover the original density is t, then after 90 per cent. mortality,

$$100x^{\mathrm{t}} = 1{,}000$$

$$\therefore\ \mathrm{t}\ \log_{10}x = \log_{10}10 = 1$$

$$\therefore\ \mathrm{t} = \frac{1}{\log_{10}x}$$

After 99 per cent. mortality,

$$10x^{\mathrm{t}'} = 1{,}000$$

$$\therefore\ \mathrm{t}'\ \log_{10}x = \log_{10}100 = 2$$

$$\therefore\ \mathrm{t}' = \frac{2}{\log_{10}x}$$

Thus, irrespective of the rate of increase (so long as it does not change), the time taken to recover from 99 per cent. mortality is twice that required for recovery from 90 per cent. mortality. In this way, the relative values of any given mortalities can be assessed, and if the value of x is known, the absolute values of the recovery times can be found.

Assuming, as we have done above, that increase is exponential, we may graph the growth of a population as a straight line, by plotting log density against time. In fig. 1, density is shown on a logarithmic scale and the time scale is reversed, to show recovery time, *i.e.*, the period required to return to the original density (set at 1,000) from any lower value. Some of the corresponding percentage mortalities are marked on the line. On the arbitrary time scale, the period required for recovery from 99·9 per cent. mortality is 10, that from 90 per cent. mortality is approximately 3·3. A series of mortality percentages in which each member has approximately twice the value of the preceding one is: 29, 50, 75, 93·75 and 99·6 per cent.

It may be worth noting that the imposition of a given percentage mortality in the course of the period of increase will have the same result, in terms of numbers reached in the given time, irrespective of whether it occurs early or late in the period. If two successive mortalities are imposed, their total effect can be calculated by multiplying together the proportions surviving. Thus if a 70 per cent. mortality is later followed by a 90 per cent. mortality, the proportion surviving will be 10 per cent. of 30 per cent., *i.e.*, 3 per cent., and the result will be the same as that of single mortality of 97 per cent.

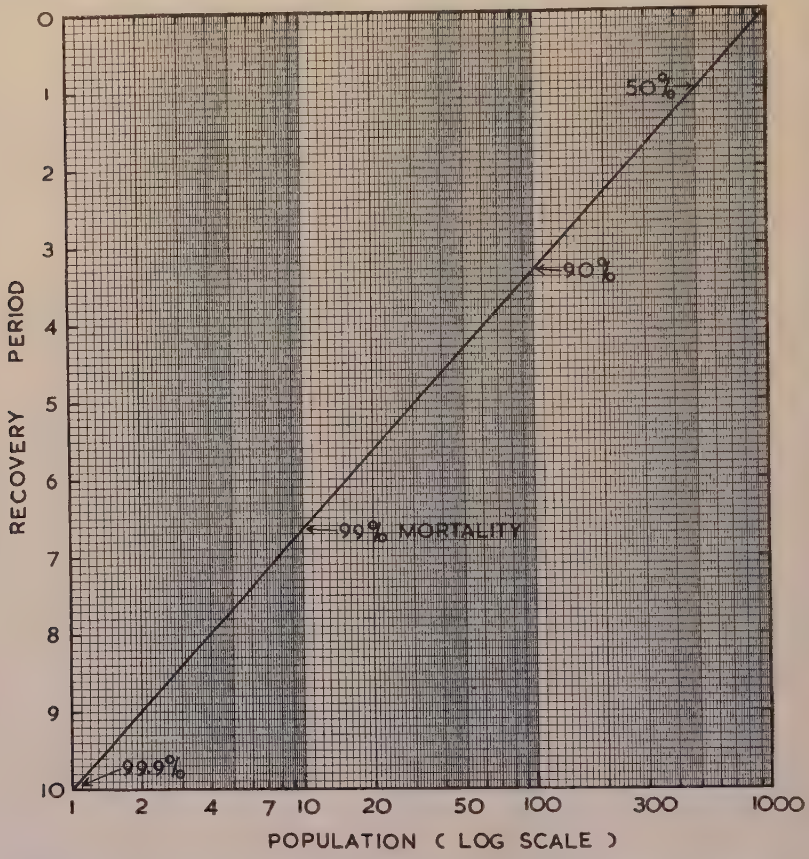


Fig. 1.—Graph of recovery periods required to regain the original population density of 1,000 after a mortality reducing the density to any lower value. The population values are plotted on a logarithmic scale. The units of time and density are arbitrary.

It may be desired to compare the periods required for return to some density level other than the original, pre-treatment one. This can be done by choosing an origin at the appropriate level above or below the top of the present fig. 1, and writing in a new scale of recovery periods, starting from the new level as zero.

In the course of increase from very low to high densities, a species may have two or three different rates of increase in succession. These may give a logarithmic graph in the form of two or three straight lines joined end to end. The above calculations can then be repeated, but each will involve a separate calculation for each linear part of the graph, giving results which, when added, represent the total time required.

When the achievement of complete mortality is not practicable, these considerations should be a useful guide in assessing the value of the treatment, or in deciding how far it is worth while to increase the dosage of fumigant. Incidentally, fig. 1 may also be used to illustrate the relative times required for an infestation to build up to a given level from different initial densities, assuming a constant rate of self-multiplication.

Summary.

Percentage mortality by itself is not a good measure of the practical value of an insecticidal treatment. In a relatively simple case, such as the fumigation of stored products, the control value can be expressed in terms of the time required for the reduced population to return to its former level of density, provided the mode of increase of the population is known.

Assuming that increase is at a regular exponential rate, the control values of different mortality percentages can be compared in terms of the calculated recovery times; thus, each of the values in the series 99·6, 93·75, 75, 50 and 29 per cent. mortality is twice as good as the one that follows it. Such relationships can be deduced from the graph provided, which is essentially a curve of constant exponential growth, made linear by the use of the logarithmic scale.

The above comparisons do not depend on the value of the constant rate of increase. If the rate of increase varies, control values can still be compared so long as it is possible to calculate the relative times needed for recovery from different levels of density.

Acknowledgements.

This note arose from a discussion with my colleague, Mr. W. Burns Brown, about work at the Pest Infestation Laboratory. It is published by permission of the Department of Scientific and Industrial Research.

Reference.

Solomon, M. E. (1953). The population dynamics of storage pests.—Trans. IXth int. Congr. Ent., **2**, pp. 235–248.

A SECOND EXPERIMENT ON TESTING THE RELATIVE EFFICIENCY OF INSECT TRAPS.

R

By C. B. Williams, R. A. French and M. M. Hosni *
Department of Entomology, Rothamsted Experimental Station, Harpenden, England.

The increased use of bait, light and suction traps in the quantitative study of insect populations, and occasionally in the attempted control of insect pests, has brought with it the necessity for a better understanding of methods of comparison of different traps. It is not possible to have two traps in the same place at the same time and, in the field at least, it is not possible to have two locations or trap sites so nearly identical that the differences can be neglected without test. So many factors affect the numbers caught in a fixed period and so many of the changes in population or activity are on a geometric scale, that running a trap for a few repetitions and lumping together the total catches does not give a result that is critical enough for our present standards.

The following account of a comparison of two types of insect light trap, and also two types of illumination, is given in some detail, more to illustrate the difficulties to be overcome, the experimental lay-out necessary and the subsequent form of analysis, than to display the actual results obtained.

In a previous paper (Williams, 1951) an experiment was described to test the relative efficiency of three light traps, and some of the difficulties and complications of such an analysis are there dealt with. At the time of this first experiment we had available two types of trap—the Rothamsted and the Robinson type (see fig. 1), and two sources of light—the ordinary electric bulb and a mercury-vapour type. Our test was incomplete, as although we had two Rothamsted traps, one with an ordinary light and one with mercury-vapour light, we could only obtain one Robinson trap, which was used with mercury-vapour light. To have completed the test we should have had a second Robinson trap with the ordinary light. Also this first test dealt with only one group of insects, the Macrolepidoptera, and only over a period of fifteen days in August 1950 during which we had the Robinson trap on loan.

In addition to the above shortcomings, we realised later that there was another variable of interest that we had overlooked, namely, the effect of a trap used one night on the insect population available to be caught the following night. For example, one type of trap might be very efficient in attracting insects to its vicinity, but less efficient in trapping them, so that there would be a large population near at hand on the following night; another type might be efficient at catching them near at hand but might not draw them from a distance, thus reducing the population available to the trap that occupied the position on the following night. In our first experiment the three traps followed each other in a regular sequence, so that any effects of this nature could not be measured.

In 1953 we decided to repeat the comparison of traps on a more complete basis with the following conditions:

(1) The four traps used were a Rothamsted type with ordinary light (A) or ultra-violet light (B), and a Robinson trap with ordinary light (C) or ultra-violet light (D). The source of ordinary light was a 200-watt electric light bulb, and of ultra-violet light was a 125-watt mercury-vapour lamp.

---

* Now at the Faculty of Agriculture, Cairo University, Giza, Egypt.

(2) Four sites were chosen, in the same woodland as that used in the previous experiment, about 60 yards apart and, owing to the fairly thick undergrowth, not directly visible from each other.
(3) The sequence of trapping was so arranged that at the end of a cycle each trap had been an equal number of nights at each site, and at each site each trap had followed itself, each other trap and a night of no trapping.
(4) All orders of insects were counted separately.
(5) The tests were spread over the summer months.

The condition in (3) that traps should follow nights of "no trapping" necessitated either a fifth site or nights of no trapping interspersed through the cycle.

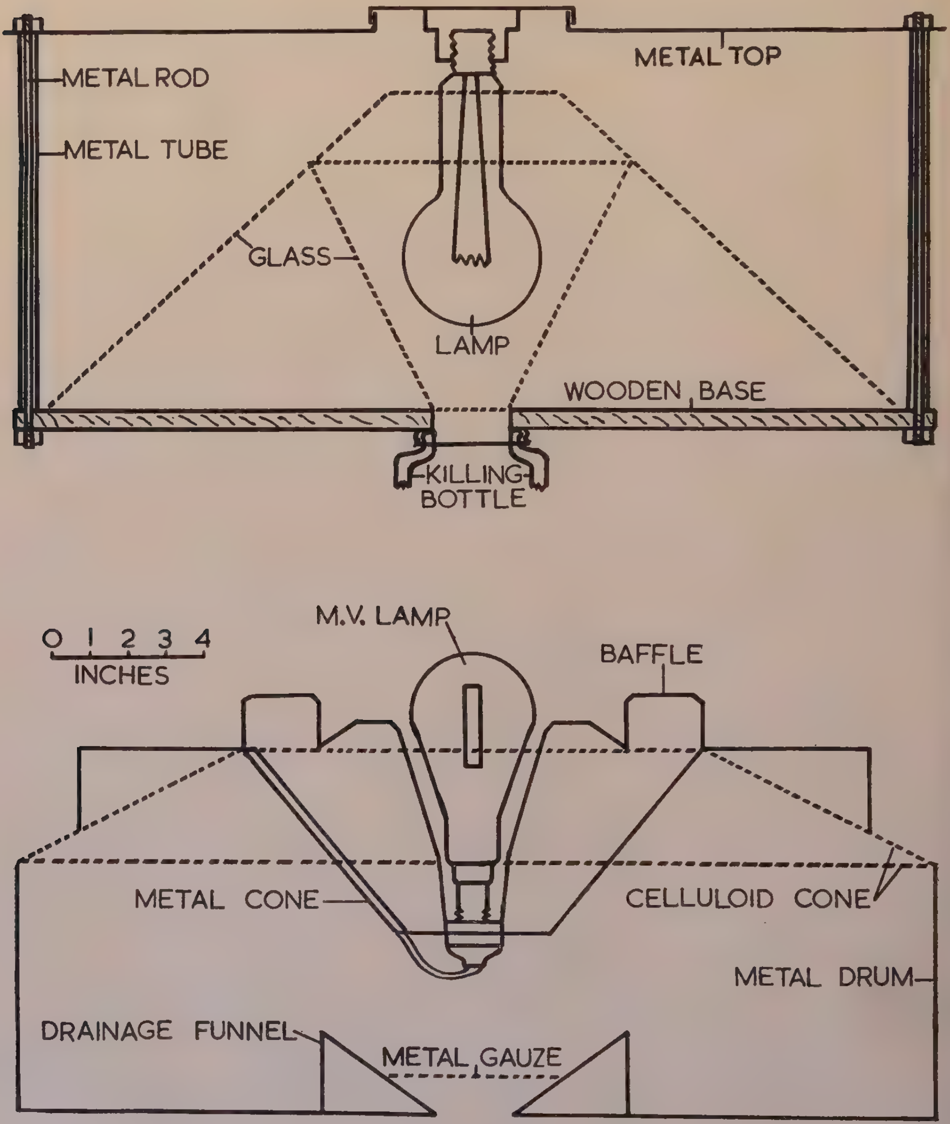

METAL ROD
METAL TUBE
METAL TOP
GLASS
LAMP
WOODEN BASE
KILLING BOTTLE
0 1 2 3 4
INCHES
M.V. LAMP
BAFFLE
METAL CONE
CELLULOID CONE
METAL DRUM
DRAINAGE FUNNEL
METAL GAUZE

Fig. 1.—Diagrammatic cross section of Rothamsted trap (above) and Robinson trap (below).

The design of such an experiment was not easy, but was finally almost completely solved by the adoption of the sequence shown in Table I, which resulted in a cycle of 24 nights, in which there were twenty nights of trapping and four of no trapping.

Table I shows the sequence in which the traps are used at each site during the first six nights of the cycle. At the end of this period, site 1 continues with the original sequence of site 2; then, after six nights more, with the original sequence of site 3, and finally with the original sequence of site 4, completing the 24-night cycle.

TABLE I.

Sequence of traps used at each site.

Site	1 (4, 3, 2)	2 (1, 4, 3)	3 (2, 1, 4)	4 (3, 2, 1)
Night 1 ..	X	X	X	X
2 ..	A	B	C	D
3 ..	B	C	D	A
4 ..	D	A	B	C
5 ..	C	D	A	B
6 ..	C	D	A	B

The figures in brackets indicate the sites at which the given trap-sequence is used in succeeding 6-night periods. X indicates no trapping and A–D the four traps.

The only drawback to the plan is that "no trapping" (and hence trapping following a night without trapping) occurs in all four sites simultaneously, thus slightly increasing the error of estimation of catches "after no trapping". The only methods that we discovered of avoiding this were either to increase the number of sites to five, or to double the length of the cycle, both of which introduced new and more undesirable sources of error.

Four complete 24-night cycles were carried out during 1953, as follows:—

(1) 11th May–3rd June
(2) 4th–27th June
(3) 19th July–12th August *
(4) 31st August–23rd September

A total of just over 370,000 insects was caught, of which approximately 17,000 were in the first cycle, 33,000 in the second, 177,600 in the third and 142,600 in the fourth. The division among the traps was approximately 72,600 in A, 192,500 in B, 21,400 in C, and 83,000 in D.

All insects were counted separately into the following groups: (1) Macrolepidoptera, further subdivided into Noctuidae, Geometridae, and "Other Families", (2) Microlepidoptera, (3) Diptera and (4) "Other Orders", which included varying numbers of Coleoptera, Heteroptera, Homoptera, Hymenoptera, Trichoptera and Neuroptera. Table II shows a typical set of results for the third cycle of trap B.

For analysis, all the catches were converted to a logarithmic scale (to two decimal places) as described in a previous paper (Williams, 1937). Table III shows the Macrolepidoptera for the four traps and the four cycles on this basis. The values were then sorted and cross-added as shown in Table IV, which gives the analysis of the Macrolepidoptera in the third cycle. In this Table, by adding

---

* By an accident, two non-trapping nights, instead of one, were inserted at one point in this cycle.

TABLE II.

Details of catches of insects in Rothamsted trap with mercury-vapour lamp (B).
Third cycle, 19th July–12th August 1953.

Night of cycle	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Total for cycle
Macrolepidoptera:																									
Noctuidae	—	43	47	21	32	32	—	12	15	24	25	16	—	5	46	81	69	75	—	15	78	49	64	150	899
Geometridae	—	77	61	17	31	37	—	43	54	27	46	16	—	38	71	92	94	139	—	55	197	72	77	173	1417
Other Families	—	6	5	4	6	5	—	1	7	5	3	0	—	5	8	5	10	10	—	5	12	8	5	10	120
Total (Macrol.)	—	126	113	42	69	74	—	56	76	56	74	32	—	48	125	178	173	224	—	75	287	129	146	333	2436
Microlepidoptera	—	207	259	38	76	111	—	28	86	44	65	4	—	124	108	195	166	271	—	91	199	167	154	265	2658
Diptera	—	4632	4461	525	702	1909	—	1940	1280	1187	1253	351	—	1120	1308	3334	1848	5724	—	2764	10000	5240	14480	25155	89213
Other Orders:																									
Coleoptera	—	1	4	2	1	8	—	4	12	2	4	2	—	6	8	9	28	42	—	1	8	3	4	10	159
Homoptera	—	26	26	0	1	4	—	6	0	2	3	3	—	9	44	88	112	194	—	13	170	14	15	98	824
Heteroptera	—	0	0	0	0	0	—	0	1	0	1	0	—	0	0	0	1	7	—	0	1	0	0	9	20
Neuroptera	—	0	0	0	0	0	—	0	0	0	0	0	—	0	0	0	0	2	—	1	1	0	0	0	4
Hymenoptera	—	18	19	4	5	11	—	8	9	5	3	8	—	7	16	23	13	45	—	14	26	19	31	34	318
Trichoptera	—	1	0	0	1	0	—	0	0	0	0	0	—	0	0	0	0	1	—	1	3	1	2	4	14
Total (Other Orders) ..	—	46	49	6	8	23	—	18	22	9	16	8	—	22	64	120	154	291	—	30	209	37	52	155	1339
Total	—	**5011**	**4882**	**611**	**855**	**2117**	—	**2042**	**1464**	**1296**	**1408**	**395**	—	**1314**	**1605**	**3827**	**2341**	**6510**	—	**2960**	**10695**	**5573**	**14832**	**25908**	**95646**

TABLE III.

Macrolepidoptera in the four traps and the four cycles.
Values as log (n + 1), where n = number caught.

Night of cycle	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Mean
First Cycle (12 May—3 June)																									
Trap A	—	0·48	0·70	0	0·78	0·60	—	0·70	0·48	1·08	0·78	0·78	—	1·28	1·61	1·00	0	1·00	—	1·23	0·70	0·30	0	0·48	0·70
B	—	0·30	0·48	0·70	1·04	1·11	—	0·48	0·70	1·34	0·90	1·11	—	1·71	1·65	1·52	1·04	1·58	—	1·26	1·11	0	0·30	0	0·92
C	—	0	1·15	0·70	1·04	0·90	—	0·90	0·60	0·90	0·95	0·85	—	1·04	1·48	1·08	1·15	0·90	—	1·18	0·85	0	0·90	1·11	0·88
D	—	1·52	1·28	1·23	0·90	1·30	—	1·30	0·90	1·36	1·08	1·11	—	1·60	1·38	1·60	1·23	1·53	—	1·18	1·04	0·30	0·48	1·30	1·18
Second Cycle (4—27 June)																									
Trap A	—	1·04	1·00	1·08	1·04	1·15	—	1·00	0·95	1·40	1·32	1·11	—	0·95	1·26	1·18	1·76	1·43	—	1·73	1·38	1·54	1·36	1·34	1·25
B	—	1·34	1·20	0·85	1·00	1·46	—	1·36	1·77	1·86	1·08	1·38	—	1·53	1·41	1·79	1·70	1·74	—	2·01	2·05	2·18	2·28	2·36	1·62
C	—	1·00	1·23	0·85	0·78	1·00	—	0·90	1·51	1·18	1·20	0·95	—	1·18	0·95	1·32	1·56	0·95	—	1·48	1·67	1·59	1·48	1·56	1·23
D	—	0	1·15	1·28	0·85	1·56	—	1·72	2·04	1·85	1·76	1·83	—	1·74	1·46	1·89	1·83	2·01	—	2·20	2·28	2·54	2·06	2·24	1·71
*Third Cycle (20 July—12 August)																									
Trap A	—	1·73	1·49	0·85	1·20	1·28	—	1·00	1·45	1·30	1·68	1·26	—	1·40	1·94	1·53	1·65	1·60	—	1·87	1·93	1·75	1·50	1·80	1·51
B	—	2·10	2·06	1·63	1·85	1·88	—	1·76	1·89	1·76	1·88	1·52	—	1·69	2·10	2·25	2·24	2·35	—	1·88	2·46	2·11	2·17	2·52	2·01
C	—	1·53	1·58	1·20	1·30	1·53	—	1·45	1·53	1·20	1·36	1·18	—	1·48	1·45	1·58	1·53	1·63	—	1·61	1·74	1·91	1·28	2·13	1·52
D	—	1·99	1·71	1·56	1·81	1·66	—	1·74	2·00	1·73	1·86	1·60	—	1·94	2·11	1·86	2·05	2·04	—	2·15	2·23	2·23	1·84	2·27	1·91
Fourth Cycle (31 Aug.—23 Sept.)																									
Trap A	—	1·15	0·95	0·90	0·60	0·85	—	0	0·30	0·70	0·95	1·42	—	0·60	1·08	0·48	0·60	0	—	0·30	0·60	0	0·70	0	0·61
B	—	1·79	1·40	0·90	1·20	1·42	—	1·40	1·08	1·43	1·04	1·61	—	1·18	1·08	1·42	1·11	0·70	—	1·30	0·85	0·70	0·90	0·48	1·15
C	—	1·23	0·90	0·95	1·15	1·08	—	1·32	1·42	0·95	0·90	1·15	—	0·48	1·04	0·85	0·85	0·48	—	1·04	1·04	0·60	0·78	0·48	0·93
D	—	1·59	1·56	1·15	1·45	1·54	—	1·34	1·58	1·32	1·04	1·70	—	1·26	1·28	1·66	1·40	1·11	—	1·30	1·32	0·60	1·28	1·15	1·30

* See also Table IV.

each of the four main rows and dividing by 20, we get (on the right) the mean log catch for each trap; by adding the five main columns and dividing by 16 we get (on the bottom row) the mean catch, irrespective of trap or site, after different traps have been used; and by adding rows A1, B1, C1 and D1, and dividing by 20 (and repeating for sites 2, 3 and 4) we get the mean catch at each site, irrespective of trap or previous night, as shown below the Table.

TABLE IV.

Analysis of Macrolepidoptera in third cycle.
Values as log (n + 1).

Trap	Site	Catch following trap:—					Mean for trap
		X	A	B	C	D	
A	1	1·73	1·60	1·65	1·30	1·93	1·51
	2	1·87	1·26	1·68	0·85	1·94	
	3	1·40	1·28	1·20	1·75	1·45	
	4	1·00	1·80	1·50	1·53	1·49	
B	1	1·76	2·06	2·52	2·17	2·25	2·01
	2	2·10	2·46	2·35	2·24	1·76	
	3	1·88	2·10	1·52	1·88	1·63	
	4	1·69	1·89	1·88	1·85	2·11	
C	1	1·46	1·91	1·52	1·52	1·28	1·52
	2	1·43	1·57	1·57	2·13	1·26	
	3	1·52	1·18	1·97	1·62	1·52	
	4	1·60	1·18	1·43	1·15	1·34	
D	1	2·11	1·85	1·54	2·11	1·59	1·91
	2	1·94	1·80	2·23	2·00	1·65	
	3	1·73	1·83	1·86	1·70	2·26	
	4	1·98	2·05	1·72	2·23	2·06	
Mean after trap		1·70	1·74	1·76	1·77	1·82	

Site means: (1) 1·79, (2) 1·80, (3) 1·66, (4) 1·67.

The final analysis for different groups of insects for the four cycles are shown in Tables V–VII. Table V tabulates the differences due to type of light and type of trap; Table VI, the effect of trapping on the previous night; and Table VII, the difference between the sites.

From Table V it will be seen, for example, that, in the Macrolepidoptera, trap D gave the maximum log catch in three of the cycles and trap B in one. On the other hand trap A was lowest in three cycles and trap C in one.

From the right half of the Macrolepidoptera table it will be seen that the mean log catch in the Rothamsted traps, irrespective of the type of light, was 1·22, and in the Robinson traps 1·34 — a difference of 0·12 or, in terms of numbers, about 25 per cent. in favour of the latter. The two types of illumination, irrespective of trap, gave a mean log of 1·08 for the ordinary electric light and 1·47 for the mercury vapour, the latter thus catching about 160 per cent. more than the former.

In the Macrolepidoptera, the differences between the traps and between the types of light were greater in the case of the family Noctuidae than in the Geometridae. In the Noctuidae, the Robinson trap caught about 66 per cent. more than the Rothamsted, and the mercury-vapour lamp about 340 per cent. more than the ordinary light. In the Geometridae there was practically no

TABLE V.

Effect of type of trap and light.

Group	Trap	Cycle				Mean	Trap type	Ordinary light	U.V. light	Mean
		1	2	3	4					
Macrolepidoptera	A	*0·70*	1·25	*1·51*	*0·61*	*1·02* (9·5)	Rothamsted	1·02	1·42	1·22 (15·6)
	B	0·92	1·62	**2·01**	1·15	1·42 (25·3)	Robinson	1·14	1·53	1·34 (20·9)
	C	0·88	*1·23*	1·52	0·93	1·14 (12·8)	Mean	1·08	1·47	
	D	**1·18**	**1·71**	1·91	**1·30**	**1·53** (32·9)		(11·0)	(28·5)	
Noctuidae	A	*0·12*	*0·79*	*0·85*	*0·26*	*0·51* (2·2)	Rothamsted	0·51	1·04	0·78 (5·0)
	B	0·40	1·39	1·55	0·82	1·04 (9·7)	Robinson	0·68	1·26	0·97 (8·3)
	C	0·34	0·90	0·94	0·52	0·68 (3·8)	Mean	0·60	1·15	
	D	**0·74**	**1·59**	**1·61**	**1·10**	**1·26** (17·2)		(3·0)	(13·1)	
Geometridae	A	*0·55*	0·91	1·38	*0·51*	*0·84* (5·9)	Rothamsted	0·84	1·08	0·96 (8·1)
	B	0·68	**1·01**	**1·77**	0·87	**1·08** (11·0)	Robinson	0·91	1·05	0·98 (8·6)
	C	0·72	*0·80*	*1·34*	0·77	0·91 (7·1)	Mean	0·88	1·07	
	D	**0·76**	0·98	1·55	**0·92**	1·05 (10·1)		(6·6)	(10·7)	
Microlepidoptera	A	*0·34*	0·71	*1·62*	0·72	*0·85* (6·1)	Rothamsted	0·85	1·21	1·03 (9·7)
	B	**0·71**	1·03	2·05	**1·06**	**1·21** (15·2)	Robinson	0·90	1·21	1·06 (10·5)
	C	0·55	*0·70*	1·67	*0·67*	0·90 (6·9)	Mean	0·88	1·21	
	D	0·63	**1·09**	**2·13**	0·98	**1·21** (15·2)		(6·6)	(15·2)	
Diptera	A	1·81	2·24	2·93	2·89	2·48 (301)	Rothamsted	2·48	2·88	2·68 (478)
	B	**2·20**	**2·63**	**3·41**	**3·29**	**2·88** (758)	Robinson	1·80	2·37	2·08 (119)
	C	*1·38*	*1·45*	*2·07*	*2·30*	*1·80* (63)	Mean	2·14	2·62	
	D	1·71	2·09	2·87	2·80	2·37 (233)		(137)	(416)	
Other Orders	A	1·06	1·06	*1·20*	1·38	1·18 (14·1)	Rothamsted	1·18	1·43	1·31 (19·4)
	B	**1·18**	**1·32**	1·58	**1·62**	**1·43** (25·9)	Robinson	1·11	1·43	1·27 (17·6)
	C	*1·05*	*0·88*	1·25	*1·27*	*1·11* (11·9)	Mean	1·15	1·43	
	D	1·14	1·25	**1·72**	1·59	**1·43** (25·9)		(13·1)	(25·9)	

Results for each group of insects and each cycle are given as the mean of the log transformations of the catches in each trap. The highest value in each column is shown in heavy type, the lowest in italics. The figures in brackets are conversions to actual numbers and represent (antilog mean log value −1).

TABLE VI.

Effect of previous trapping.

Previous trap	Cycle				Mean	Cycle				Mean
	1	2	3	4		1	2	3	4	
	Macrolepidoptera					Noctuidae				
X	1·01	*1·32*	*1·70*	**1·08**	1·28 (18·0)	0·41	*1·05*	*1·16*	**0·73**	*0·84* (5·9)
A	*0·82*	1·43	1·74	*0·95*	*1·24* (16·4)	0·40	1·11	1·25	*0·59*	*0·84* (5·9)
B	0·87	**1·58**	1·76	1·01	1·31 (19·4)	*0·37*	**1·31**	**1·29**	0·68	**0·91** (7·1)
C	0·88	1·42	1·77	*0·95*	1·26 (17·2)	0·38	1·16	1·27	0·65	0·87 (6·4)
D	**1·02**	1·50	**1·82**	1·00	**1·34** (20·9)	**0·44**	1·20	1·20	0·72	0·89 (6·8)
	Geometridae					Microlepidoptera				
X	**0·78**	0·90	1·51	**0·86**	**1·01** (9·2)	0·61	*0·67*	*1·80*	**1·00**	1·02 (9·5)
A	*0·55*	0·91	1·52	0·75	*0·93* (7·5)	*0·54*	**0·96**	**1·97**	0·95	**1·11** (12·0)
B	0·67	**1·02**	1·50	0·75	0·99 (8·8)	0·55	0·94	1·83	*0·73*	*1·01* (9·2)
C	0·61	*0·86*	**1·54**	*0·70*	*0·93* (7·5)	0·61	0·92	1·88	0·77	1·05 (10·2)
D	0·77	0·93	*1·48*	0·78	0·99 (8·8)	**0·72**	0·92	1·83	0·84	1·08 (11·0)
	Diptera					Other Orders				
X	**1·96**	*1·90*	2·84	**3·02**	**2·43** (268)	**1·18**	*0·93*	1·37	**1·53**	*1·25* (16·8)
A	*1·65*	2·17	*2·72*	2·79	*2·34* (218)	*1·04*	1·20	1·48	1·52	**1·31** (19·4)
B	1·74	2·17	2·90	2·76	2·39 (245)	1·07	1·11	1·46	*1·37*	*1·25* (16·8)
C	1·79	2·10	**2·91**	2·83	2·41 (256)	1·11	**1·22**	**1·51**	1·44	1·32 (19·9)
D	1·75	**2·18**	2·78	*2·73*	2·36 (228)	1·13	1·18	*1·34*	1·47	1·28 (18·1)

Results for each group of insects and each cycle are given as the mean of the log transformations of the catches on the night following each type of trapping. The highest value in each column is shown in heavy type, the lowest in italics. The figures in brackets are conversions to actual numbers and represent (antilog mean log value −1).

TABLE VII.

Effect of site.

Site	Cycle				Mean	Cycle				Mean
	1	2	3	4		1	2	3	4	
	Macrolepidoptera					Noctuidae				
1	*0·78*	**1·53**	1·79	*0·96*	1·27 (17·6)	*0·31*	**1·29**	**1·30**	0·71	0·90 (6·9)
2	**1·00**	1·52	**1·80**	**1·07**	**1·35** (21·4)	0·41	1·20	1·28	**0·74**	**0·91** (7·1)
3	0·94	1·39	*1·66*	0·99	1·25 (16·8)	0·39	*1·08*	*1·17*	*0·60*	*0·81* (5·5)
4	0·96	*1·32*	1·67	0·98	*1·23* (15·9)	**0·43**	1·10	1·19	0·65	0·84 (5·9)
	Geometridae					Microlepidoptera				
1	*0·56*	0·98	1·60	*0·69*	0·96 (8·1)	**0·75**	**0·96**	1·90	0·86	**1·12** (12·2)
2	**0·75**	**1·01**	**1·59**	**0·83**	**1·05** (10·2)	*0·44*	0·93	**1·97**	**0·94**	1·07 (10·8)
3	0·67	0·86	*1·41*	0·81	*0·94* (7·7)	0·62	0·83	*1·73*	*0·81*	*1·00* (9·0)
4	0·74	*0·84*	1·44	0·75	0·94 (7·7)	0·66	*0·82*	1·88	*0·81*	1·04 (10·0)
	Diptera					Other Orders				
1	1·80	2·12	**2·94**	**2·91**	**2·44** (274)	1·12	*1·07*	*1·30*	**1·54**	1·26 (17·2)
2	*1·66*	*2·02*	2·79	*2·75*	*2·31* (203)	*0·92*	1·10	1·53	1·44	*1·25* (16·8)
3	1·80	**2·19**	*2·75*	2·82	2·39 (245)	1·08	**1·24**	1·36	*1·39*	1·27 (17·6)
4	**1·84**	2·09	2·81	2·81	2·39 (245)	**1·31**	1·16	**1·54**	1·49	**1·48** (29·2)

Results for each group of insects and each cycle are given as the mean of the log transformations of the catches at each site. The highest value in each column is shown in heavy type, the lowest in italics. The figures in brackets are conversions to actual numbers and represent (antilog mean log value −1).

difference between the traps, but the mercury-vapour lamp was again distinctly more attractive.

In the Microlepidoptera, the Diptera, and in the other orders of insects, the difference between the lights remained high, the catch with ultra-violet being from two to three times that with ordinary light. But while in the first and last of these groups there was little difference in the efficiency of the two types of traps, in the case of the Diptera the Rothamsted trap caught four times as many insects as the Robinson trap.

Thus all groups of insects show distinctly more attraction to the mercury-vapour light, but the relative efficiency of the trap types varies according to the kind of insect. This will be discussed more fully later.

Table VI shows what effect the type of trap used (or the absence of trapping) on one night has on the catch of the following night. The mean log catch of the five independent groups (*i.e.*, excluding the Macrolepidoptera) on the night after no trapping is exactly the same as the mean catch after all other traps. There appears, therefore, to be no consistent after-effect of trapping.

In Table VII the effect of site is shown, and this is also quite inconsistent. Within the groups there was occasionally slight evidence of consistency—in the Macrolepidoptera, for example, Site 2 was the most productive, or nearly so, in all four cycles, and analysis showed that this was due to consistent maxima in this site in all cycles in the Geometridae, and maxima or near maxima in all cycles in the Noctuidae.

TABLE VIII.

Analysis of variance in the first cycle.

Source of Variation	Degrees of freedom	Total sum of squares	Mean square	*P*	% of variance explained
Macrolepidoptera					
Total	79	15·8521	—	—	
Between nights	19	8·6434	0·4549	<0·001	54·5
Between sites	3	0·5535	0·1845	<0·10 >0·05	3·5
Between traps	3	2·3654	0·7885	<0·001	15·0
Effect of previous trap ..	4	0·5114	0·1278	<0·20 >0·10	3·0
Residual error	50	3·7784	0·0756	—	24·0
Diptera					
Total	79	30·0573	—	—	
Between nights	19	19·1292	1·0068	<0·001	63·5
Between sites	3	0·3946	0·1315	<0·10 >0·05	1·5
Between traps	3	6·9515	2·3172	< 0·001	23·0
Effect of previous trap ..	4	0·8211	0·2053	0·01	2·5
Residual error	50	2·7609	0·0552	—	9·5

Original data from Table III, re-arranged as in Table IV.

On the whole, however, there is little evidence of differences between the sites, a result which is gratifying in the present case, as they were chosen to be as similar as possible, so as to avoid interference with the main problem, which was to test the difference between the traps.

The significance of the above results can be tested by means of an analysis of variance, which is most easily done in two stages, first within the single cycles and then between the four cycles.

Table VIII shows as an example the analysis of variance of the Macrolepidoptera, and of the Diptera, in the first cycle. With a total of 80 trap–nights (20 nights with four traps) there are 79 degrees of freedom. In the Macrolepidoptera the difference between nights is, as would be expected, very highly significant at well under 1 in 1,000 and the difference between the traps attains an even higher level of significance. On the other hand, the effect of site is scarcely significant, the probability lying between 1 in 10 and 1 in 20, while the effect of the previous night's trapping does not even reach the 1 in 10 level of

TABLE IX.

Analysis of variance between the four cycles.

Source of Variation	Degrees of freedom	Sum of squares	Mean square
(1) Traps and Cycles, Macrolepidoptera (Table V)			
Total	15	2·4978	—
Between traps	3	0·6638	0·2213**
Between cycles	3	1·7482	0·5827**
Residual error	9	0·0858	0·0095
(2) Traps and Cycles, Diptera			
Total	15	5·8079	—
Between traps	3	2·3869	0·7956**
Between cycles	3	3·3209	1·1070**
Residual error	9	0·1001	0·0111
(3) Previous Traps and Cycles, Macrolepidoptera (Table VI)			
Total	19	2·3023	—
Between previous traps	4	0·0175	0·0044
Between cycles	3	2·2387	0·7462**
Residual error	12	0·0561	0·0049
(4) Previous Traps and Cycles, Diptera			
Total	19	4·4661	—
Between previous traps	4	0·0239	0·0060
Between cycles	3	4·4132	1·3711**
Residual error	12	0·0390	0·0033
(5) Sites and Cycles, Macrolepidoptera (Table VII)			
Total	15	1·8269	—
Between sites	3	0·0322	0·0107
Between cycles	3	1·7435	0·5812**
Residual error	9	0·0512	0·0057
(6) Sites and Cycles, Diptera			
Total	15	3·4000	—
Between sites	3	0·0388	0·0127*
Between cycles	3	3·3331	1·1110**
Residual error	9	0·0281	0·0031

** Highly significant ($P < 0·01$). * Significant ($P < 0·05$).

significance. Of the total variation, 54·5 per cent. is due to the difference between the nights and 15 per cent. to the difference between the traps.

In the Diptera, the results are very similar except that there is some indication of a significant difference between the "previous trap" effects. Rather more of the total variance (63·5%) is due to the difference between nights, and also rather more (23%) to the difference between the traps.

Table IX shows six examples of the analysis of variance between the four cycles for the Macrolepidoptera and for the Diptera, in each case for traps, for previous trapping and for site. In every case there are, as expected, highly significant differences between the cycles. The variation between traps is highly significant in both groups, but the effect of the previous night's trapping is significant in neither; the site effect is barely significant in the Lepidoptera but just significant in the Diptera.

Discussion.

Although the object of the present paper is to show the layout of a trap-testing experiment, rather than to discuss our particular results in detail, it may be interesting to point out that the essential differences between the two types of trap (see diagrammatic cross sections in fig. 1) are that in the Rothamsted design the light is inside the trap and there is an opaque roof, whereas in the Robinson design the light is just above the trap and there is no roof. The roof was originally put on the first type to keep the rain from entering the killing bottle; in the Robinson type the rain is allowed to enter, but is drained away below. The absence of a roof allows the light to be seen by insects passing overhead and so may result in greater efficiency. The position of the light may be responsible for some of the other differences mentioned above. In the Robinson design, the light is just above the entry to the trap proper, so insects do not enter it unless they fly beyond the light. This occurrence is likely to depend on their momentum, and hence on their size and speed. Thus we find that the heavier-bodied, fast-flying moths of the family Noctuidae show the greatest difference in favour of the Robinson trap, while the smaller and lighter Geometridae, the Microlepidoptera and the other orders show less difference. The very small and weak-flying nocturnal Diptera can be seen at night moving round and round the light of the Robinson trap in a cloud a foot or so above the light, without going in, and this may well be associated with the relatively low captures of Diptera in this trap. It is possible that small alterations may produce a trap with the advantages of both types, and work is at present planned in this direction. We are proposing to test the Rothamsted trap with a smaller roof, and we have heard, since drafting this paper, that workers in Holland have increased the efficiency of the Robinson trap, in respect of catching Diptera, by adding a small roof.

Thus, the general conclusions for the trap-type and illumination comparison are, first, that a 125 watt mercury-vapour lamp gives catches that are from one-and-a-half to three times as large as those with the 200 watt ordinary bulb, according to the group of insects caught; and, secondly, that the Robinson trap is definitely better for catching the heavier, stronger-flying insects, while for the smallest insects the Rothamsted type is superior.

Conclusions.

The layout of any experiment for the comparison of insect traps depends primarily on the number of types to be tested, but in the field it also depends on the fact that no two locations are identical and no two repetitions give the same result. One also has to decide beforehand if it is safe to neglect the effect of any one trapping on the population and hence on the numbers available for the trap that follows.

With two traps and two sites, neglecting after-effects, the sequence ABAB in one site and BABA in the other is the simplest. If the after-effects are to be studied, then the sequence AABBAABB in one site and the reverse in the other covers all possibilities every four days, instead of every two as in the first case.

With three traps and three locations, the sequences ABC, BCA and CAB, as described in the earlier paper, are sufficient if after-effects can be neglected, giving a cycle every three days.

With four traps (or two different traps and two different types of lighting), four sites and the sequences ABCD, BCDA, etc., give a complete cycle every four days if after-effects are neglected, but as soon as one allows for these, the complex layout of the present paper is necessary, with a cycle once every twenty-four days.

Summary.

The paper describes the layout and analysis of a test of two types of insect light-trap, the Rothamsted and the Robinson, and two types of illumination. The layout consisted of four variations of the sequence of six nights X A B C D D (X being a night of no trapping and A–D the four traps) in each of four sites in a small woodland. At the end of a complete cycle of 24 nights there had been four nights without trapping; each trap had been an equal number of times in each site; and each trap had followed all four trap-types, and also no-trapping, an equal number of times. The complete cycle was repeated four times at intervals between May and September. All insects captured were sorted into orders and counted and each order was analysed separately. By analysis of variance (after transforming the numbers caught to a logarithmic scale) it was possible to show separately the effect of differences, (1) between nights, (2) between sites, (3) between types of trap, (4) between types of light, and, (5) between cycles, and also the effect (if any) of the previous night's trapping. It was found that ultra-violet light was more efficient for all orders than ordinary electric light, that the Robinson type of trap was more efficient for the larger Lepidoptera but much less efficient for the small Diptera, but that there was no regular effect of the previous night's trapping. The largest source of variation was the difference between nights: difference between locations was small.

References.

Williams, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems.—Ann. appl. Biol., **24**, pp. 404–414.

Williams, C. B. (1951). Comparing the efficiency of insect traps.—Bull. ent. Res., **42**, pp. 513–517.

PHYSIOLOGICAL ACTION OF DRUGS AND INSECTICIDES ON INSECTS.

By Mohan Babu Naidu, M.Sc., Ph.D. (London)
London School of Hygiene and Tropical Medicine.

Previous work on the physiological action of drugs and insecticides on insects has been mostly concerned with their effect and comparatively little attention has been paid towards their site and mode of action. The findings of Roeder & Roeder (1939), Means (1942), Chadwick & Hill (1947), Tobias, Kollros & Savit (1946), Richards & Cutkomp (1945), Orser & Brown (1951) and Krijgsman & Krijgsman-Berger (1951), show the presence of acetylcholine in the nervous tissues of insects and its importance as the chemical mediator. It is also shown that the toxicity of some of the organophosphorus compounds like TEPP, HETP and parathion is due to their anticholinesterase activity. On the other hand, Hamilton (1939), Hopf (1952) and Lord & Potter (1951) conclude that the toxicity of TEPP is not due to anticholinesterase inhibition and they very much doubt the importance of acetylcholine and the existence of cholinergic and adrenergic processes in insects.

The present work was undertaken not only to clarify the conflicting views on the presence of cholinergic and adrenergic systems in insects, but also to investigate the physiological action of certain insecticides, which have not been studied with reference to their site and mode of action.

Materials and Method.

Selection of physiological solution and test insect.

Physiological solutions employed by Pringle (1938), Krijgsman, Dresden & Berger (1950) were tested on the isolated heart preparations of adult *Blatta orientalis* L., *Periplaneta americana* (L.) and locusts. Of all the species tested, it was observed that the heart preparation of *Periplaneta* alone maintains a more or less constant rate of frequency for several hours in the physiological solution adopted by Krijgsman, Dresden & Berger (1950). Therefore the present paper deals only with the isolated heart preparation of adult laboratory-bred *Periplaneta* and the Ringer solution described by Krijgsman, Dresden & Berger.

Formula of the physiological solution:—

NaCl 9·82 gm., KCl 0·77 gm., $CaCl_2$ 0·5 gm.
$NaHCO_3$ 0·18 gm., NaH_2PO_4 0·01 gm.,
dextrose 1·0 gm. and distilled water 1,000 cc.

Drugs and insecticides used.

Acetylcholine chloride, atropine sulphate, nicotine, hexamethonium iodide, adrenaline, nor-adrenaline hydrochloride, ergotamine, eserine, pyrethrum, rotenone, pure parathion, paraoxon and p,p′DDT. All the drugs used are soluble in the physiological solution but the insecticides used were insoluble in it: hence they were dissolved in acetone and the required concentrations added to the physiological solution. In no case did the quantity of acetone exceed more than 0·2 per cent. of the volume of the physiological solution, which has no detrimental effect on the heart. Fresh solutions of the drugs and insecticides were always used for the experiments. In general, the concentration of substances in liquid form were used as v/v and those in solid form as w/v.

The cockroach heart preparation and the use of the apparatus.

The cockroach was immersed in tap water until it became inactive. The head, legs and wings were then cut off. The decapitated insect was pinned to a wax plate dorsal side down. The heart was exposed by removing the sternites and the digestive and reproductive organs. This preparation was entirely free from the ventral chain and the ganglion of the head. Consequently the action of the drugs and insecticides was restricted to the heart and its pacemaker.

After isolation in this way, the heart generally stops or beats irregularly at first. In most cases the post-operative shock is overcome in about an hour and the heart then beats regularly for several hours.

The apparatus used for observing the heart-beat is shown in fig. 1. The isolated heart preparation is introduced vertically into the experimental tube containing aerated physiological solution maintained at a temperature of 29°C. and having a pH of 7·0–7·2. A constant stream of the physiological solution is allowed to drip from the reservoir (R) into the funnel which reaches down to the bottom of the experimental tube; otherwise a decrease in the rate of pulsation occurs. The heart-beat is observed by means of a binocular microscope and its frequency is determined with a stop-watch. Observations were restricted to the part of the heart which lies between the fourth and fifth abdominal segments. A period of one minute is employed for each count and the counts were made at frequent intervals. There is a considerable variation in the rate of pulsation among individuals; about 80 per cent. of the preparations maintain a frequency between 90 and 130 per minute.

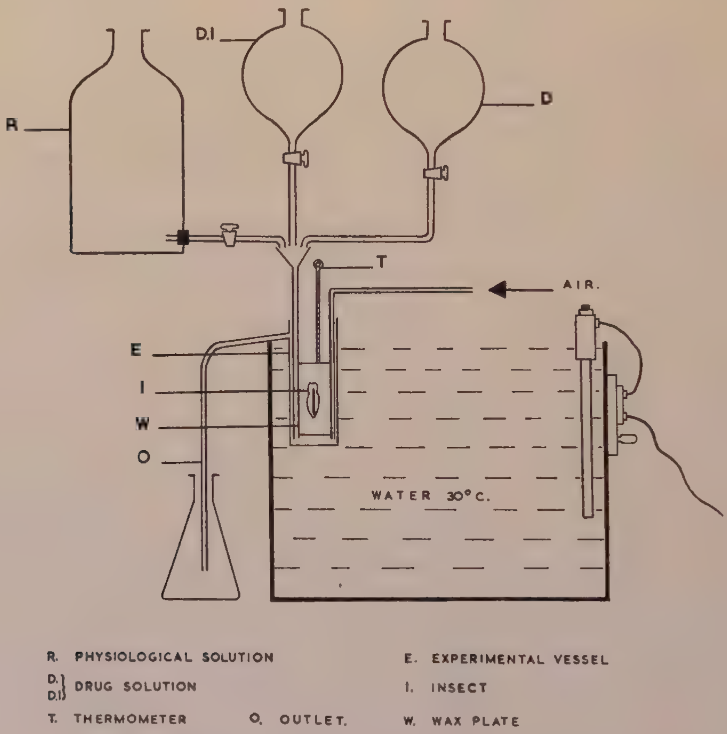


Fig. 1.—Apparatus for studying the action of drugs and insecticides on the isolated heart of the cockroach.

To test a particular solution of the drug or insecticide, it was first heated to 29°C. and then poured rapidly into the funnel (D or D.1), whence it flowed immediately into the experimental tube, sufficient being added to replace about twice the volume of solution present in the experimental tube. Thereafter, the solution under test continued to drip into the funnel at a constant rate (115–120 drops per minute). The conclusions as to the action of any drug or insecticide are based on trials on at least five different heart preparations. In the figures which follow, the mean result of five (or more) tests provides the value for each point shown on the graph. Arrows in the graphs indicate the point of addition of a drug.

Anatomy of the cockroach heart and its contractile and pacemaker mechanism.

The cockroach heart is a long, narrow tube closed posteriorly, extending from the caudal extremity of the body through the thorax and terminating in the head. It consists of 13 segments with a pair of lateral inlets (ostia) in each segment. Pairs of alary muscles arise from the terga and meet beneath the heart with those of the corresponding muscle of the opposite side of the body (Imms, 1948).

The anatomical researches by Alexandrowicz (1926) in *B. orientalis* and McIndoo & Smithson (1945) in *P. americana*, and the pharmacological investigations by Prosser (1942) on arthropods, Davenport (1949) on *Stenopelmatus*, and Krijgsman & Krijgsman-Berger (1951) on *P. americana* strongly suggest that the pacemaker mechanism of *P. americana* is neurogenic in nature and that diastolic and systolic contractions of the heart are inherent qualities of the heart itself.

Results.

Action of individual drugs.

Effect of nicotine (NIC).—Nicotine at 10^{-2} causes an immediate cessation of the heart in systole without any initial increase in the frequency of the beat, while 5×10^{-3} causes a slow decline in the rate of heart-beat with periodic pauses in systole and eventually cessation in systole.

Nicotine (5×10^{-5}) causes an immediate increase in the frequency of the heart-beat (fig. 3) followed by depression, with reduced amplitude. During later stages of the depression, the heart-beat becomes irregular and unco-ordinated. At a dilution of 3×10^{-7} nicotine, there is a slight increase in the frequency which is maintained for 4–5 hours before the final decline of frequency begins.

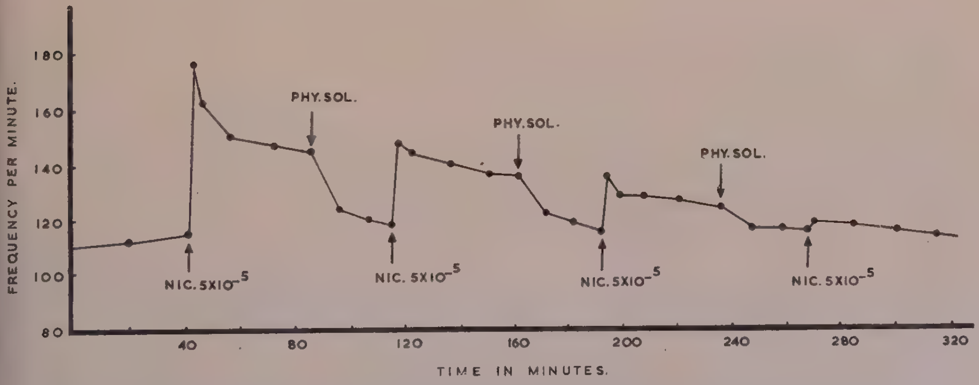


Fig. 2.—Progressive paralysing effect of nicotine on the ganglia present on the lateral nerve of the isolated heart of the cockroach. (The paralysing effect by nicotine is measured in terms of the frequency of the heart-beat.)

Effect of prolonged action of nicotine.—After 40 minutes of treatment with nicotine 5×10^{-5}, which causes initial stimulation, perfusion with physiological solution soon restores the heart-beat to approximately its original frequency. By alternate washing with the physiological solution followed by treatment with nicotine, at intervals of 40 minutes, it is observed that the increase of frequency caused by the addition of nicotine diminished on each successive occasion, and at the end of four hours, when the fourth administration of nicotine is given, little or no stimulation of the heart is evident (fig. 2). Instead, the heart continues to beat rather irregularly and the frequency slowly declines. The point at which no increase of frequency of the beat is caused, when nicotine 5×10^{-5} is added, varies with the individual insect. Generally it requires three hours of contact with the drug.

This action of nicotine, by which repeated administration leads to a progressive block of its stimulant action, corresponds closely to its action in mammals, in which the stimulant phase of its effects are soon followed by an antagonism to its own stimulant action or to that of other ganglion-exciting drugs. It may be asked why the stimulant effect of nicotine progressively declined. Perhaps the successive additions of the drug were either affecting certain of the ganglia which had not been paralysed previously, or all the ganglia had only been partially paralysed by earlier treatment and their paralysis increased progressively with each treatment. It appears that the former suggestion is more probable. This view is further supported by the findings of Prosser (1940). He noted in crayfish that all the ganglia are not blocked by nicotine simultaneously, but they drop out one by one. However after prolonged washing with the physiological solution, nicotine 5×10^{-5} induces a marked increase of the rate of heart-beat,

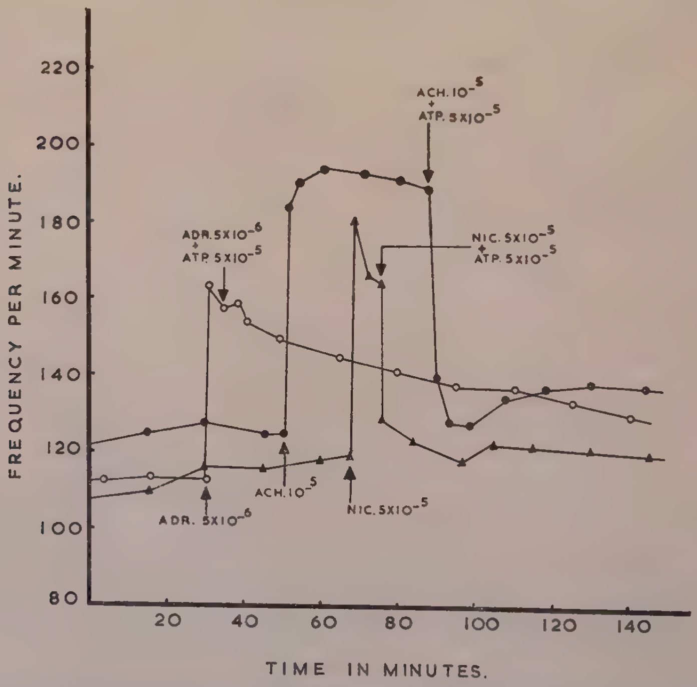


Fig. 3.—The effect of nicotine, acetylcholine and adrenaline, and antagonism between atropine on the one hand and acetylcholine, nicotine and adrenaline on the other, on the isolated heart of the cockroach.

thus showing that the paralysis of the ganglia induced by the drug is of a temporary nature.

Effect of acetylcholine (ACH).—ACH (10^{-3} to 10^{-5}) causes an immediate increase of frequency (fig. 3) followed by a slow decline. The heart beats vigorously with increased amplitude. A dilution of 10^{-8} causes a slight increase of frequency which continues for two to three hours, whilst a dilution of 2×10^{-9} sometimes, but not always, induces an increase of frequency which may continue for several hours. This concentration of ACH appears to be the threshold concentration.

The action of ACH at all concentrations is reversible when washed with the physiological solution but, after treatment for an hour at the higher concentration the original frequency is not attained.

Effect of atropine (ATP).—An immediate depression of the frequency of the heart-beat occurs on the addition of atropine 2×10^{-3} and continues until the heart stops in diastole. A concentration of 5×10^{-4} produces a steady decline of frequency with periodic pauses in diastole. At a concentration of 10^{-4} a temporary increase in the frequency of the heart-beat is followed by a progressive depression. Finally, with 5×10^{-5} atropine, an immediate increase in the frequency of the heart-beat occurs and continues for two hours, when a terminal decline in the frequency of the heart-beat follows and continues for two hours, after which the rate declines still further.

The action of atropine is reversible, provided the treatment period does not exceed 45 minutes and the concentration of the drug does not exceed 4×10^{-4}.

Effect of adrenaline (ADR).—Adrenaline (10^{-5} to 5×10^{-6}) induces an immediate increase in the frequency of the heart-beat (fig. 3), initially with irregularity, followed by a decline and finally the heart stops in systole. Adrenaline at 10^{-9} induces a slight increase of frequency in some cases and this dilution appears to be the threshold concentration. The effects of nor-adrenaline 5×10^{-6} are similar to that of adrenaline at the same concentration..

The action of adrenaline is reversible at lower concentrations but at higher concentrations the original frequency is not attained after washing with the physiological solution.

The action of adrenaline differs from that of ACH in two ways. First, the acceleration of the heart is much less and not well sustained with adrenaline and actually may pass over into slowing; secondly, the heart stops in systole and not diastole as with ACH.

Effect of ergotamine (ERG).—Ergotamine (5×10^{-6} to 3×10^{-6}) causes an initial increase in the frequency of the heart-beat followed by depression. During depression the heart beats irregularly, with reduced amplitude.

Effect of eserine (ESR).—Eserine (10^{-5} to 5×10^{-6}) induces an immediate increase in the frequency of the heart-beat, which persists for some time. The heart beats vigorously with increased amplitude; but eventually a slow decline in the rate of frequency occurs. At a concentration of 10^{-8} a slight increase in the frequency occurs which after persisting at a certain level steadily declines.

The action of eserine is reversible. In many respects the effect produced by eserine appears to be similar to that of acetylcholine.

Effect of hexamethonium (HEX).—Hexamethonium (5×10^{-5} and 10^{-5}) causes no changes in the rate of heart-beat in many cases, but in some a slight increase in the frequency is observed.

Synergism and antagonism of drugs.

The increase in the frequency of the heart-beat caused by ACH 10^{-5} is abolished immediately by the addition of atropine 5×10^{-5} (fig. 3). Also, after treatment with atropine 5×10^{-5}, ACH 10^{-5} does not have any effect on the rate of heart-beat. Similarly, addition of ACH 10^{-3} causes an immediate increase in the frequency of the heart-beat, but not after preliminary treatment with atropine 3 × 10^{-4}.

Ergotamine 3 × 10^{-6} does not modify the action of ACH 10^{-5}, though it antagonises the action of adrenaline 5 × 10^{-6} and atropine 5 × 10^{-5} does not. Previous treatment with hexamethonium 5 × 10^{-5} does not produce any significant effect on the actions of adrenaline 5 × 10^{-6}, ergotamine 3 × 10^{-6} (fig. 5) and ACH 10^{-5}. But it is observed that hexamethonium 5 × 10^{-5} blocks completely the action of 10^{-5} nicotine.

Atropine 5 × 10^{-5} is found to reduce considerably the action of nicotine 5 × 10^{-5} (fig. 3). Similarly, by previous treatment with atropine 5 × 10^{-5} for 30 minutes the increase in the frequency of the heart-beat caused by nicotine 5 × 10^{-5} is much less when compared with its normal effect. On the other hand the increase in the frequency of the heart-beat caused by nicotine 5 × 10^{-5} is not modified by previous treatment with ergotamine 3 × 10^{-6}.

ACH 5 × 10^{-11} which normally does not produce any effect on the frequency of the heart-beat, on addition to the heart preparation previously treated with eserine 10^{-8} produces a rise in frequency. Similarly, nicotine 3 × 10^{-7} which induces a slight increase in the rate of beat, causes an immediate appreciable increase in the frequency in a preparation previously treated with eserine 10^{-5}. But eserine does not alter the action of adrenaline 10^{-9}. Atropine 10^{-5} is found to antagonise the action of eserine 10^{-5}.

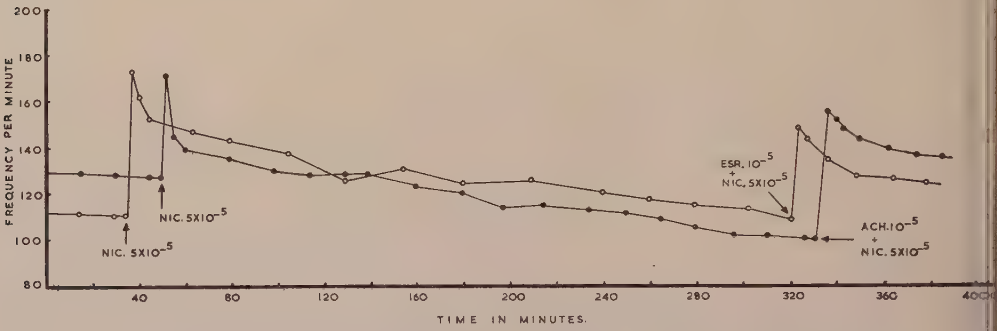


Fig. 4.—The effect of acetylcholine and eserine on the frequency of the beat of the isolated heart of the cockroach after prolonged exposure to nicotine.

Previous treatment with nicotine 5 × 10^{-5} continuously for four hours, which paralyses the ganglion cells, does not modify the action of ACH 10^{-5} (fig. 4), adrenaline 5 × 10^{-6} or ergotamine 3 × 10^{-6} (fig. 5), but it abolishes the acceleration caused by atropine 5 × 10^{-5} (fig. 5).

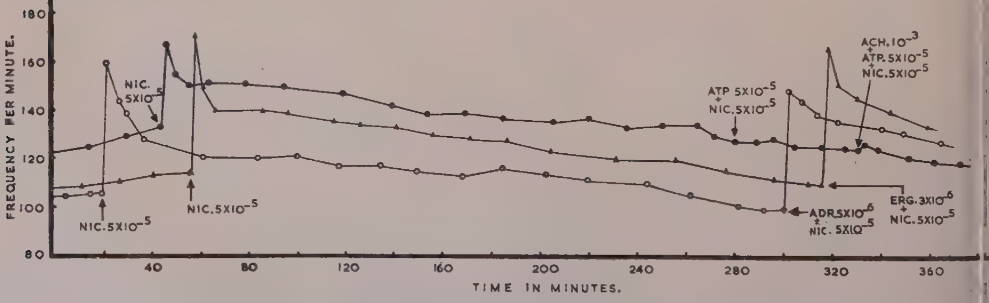


Fig. 5.—The effect of adrenaline, ergotamine, atropine and high concentration of acetylcholine with atropine on the frequency of the beat of the isolated heart of the cockroach after prolonged exposure to nicotine.

Further studies on synergism and antagonism of drugs.—After treatment with nicotine 5×10^{-5} for about four hours, additional treatment with atropine 5×10^{-5} is introduced; after 50 minutes of this treatment with atropine, ACH 10^{-3} is added. This does not produce any increase in the frequency of the heart-beat, which it would have done without additional treatment with atropine (see above).

Effect of insecticides alone and with drugs.

Pyrethrum (PYR).—Pyrethrum * at a concentration of 4×10^{-7} causes an immediate depression in the frequency of the heart-beat, which continues steadily later. But 10^{-7} pyrethrum induces a temporary initial increase of frequency whereas 10^{-8} causes an increase of frequency which is maintained for some time before a terminal decline in the rate of beat. At all concentrations of pyrethrum the heart beats irregularly, accompanied by an increase in the amplitude and occasional pause in diastole.

The action of pyrethrum is reversible in all concentrations, although after an hour's treatment at a concentration 2×10^{-6} the heart does not recover its original frequency on washing with the physiological solution.

After treatment with pyrethrum 10^{-8} for 40 minutes the addition of nicotine 5×10^{-5} induces only a slight increase of frequency, as compared with the response when nicotine alone is applied, followed by depression (fig. 6). On the other hand, after treatment with nicotine for 220 min. continuously, addition of pyrethrum 10^{-8} causes an immediate increase in the rate of frequency of the heart-beat which continues for 15 to 20 minutes and then declines to the frequency prior to the addition of pyrethrum (fig. 7).

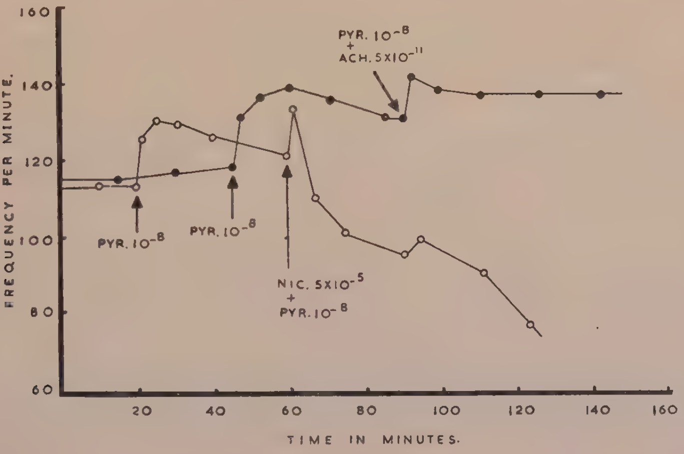


Fig. 6.—The effect of nicotine and acetylcholine on the frequency of the beat of the isolated heart of the cockroach after pyrethrum treatment.

Atropine 5×10^{-5} partially blocks the action of pyrethrum 10^{-8} while 3×10^{-4} atropine abolishes it completely. Treatment with nicotine 5×10^{-5} for three hours continuously and then additional treatment with atropine 5×10^{-5} abolishes completely the action of pyrethrum 10^{-8} when added forty minutes later (fig. 7). This is contrary to the results in the first series of these experiments, in which pyrethrum 10^{-8} causes an increase in the frequency when it is added after either atropine (low concentration) or nicotine (prolonged action) separately. This indicates that the acceleration of the heart-beat caused by pyrethrum in the presence of atropine (low concentration) is due to its action on the ganglia. Pyrethrum 10^{-8}, if followed by ACH 5×10^{-11}, which normally does not produce any increase of frequency, is found to potentiate the action of the latter.

---

* A liquid extract containing 25 per cent. pyrethrins.

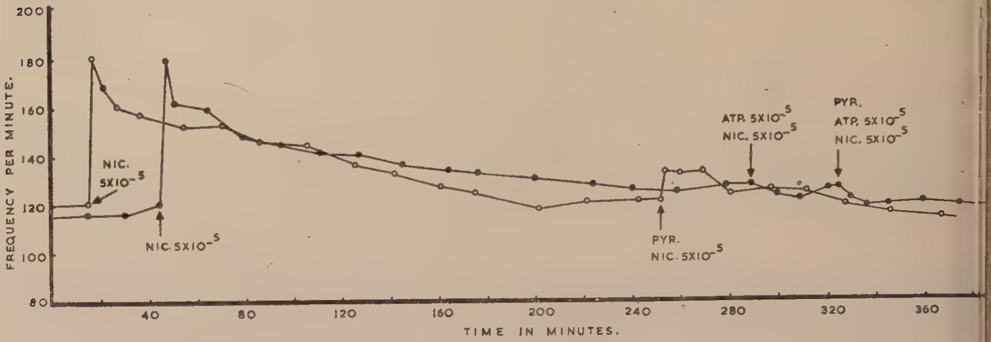


Fig. 7.—The effect of pyrethrum and atropine on the rate of frequency of the isolated heart of the cockroach after prolonged nicotine, independently and in combination.

Rotenone (ROT).—Rotenone in all concentrations from 6×10^{-7} to 14×10^{-6} results in a decrease of frequency and eventual cessation of the heart in diastole. It is observed that the decline in the rate of frequency of the heart-beat does not occur until some time after the addition of the insecticide. The fall in the frequency is usually distinct, being non-rhythmical and usually associated with diastolic contractions.

The time-lag between the administration of rotenone solutions of different concentrations and the appearance of its effect on the frequency of the heart-beat is shown in Table I.

TABLE I.

Time-lag between administration of rotenone solutions of different concentrations and appearance of their effects.

Concentration of rotenone	Time-lag in minutes between addition of rotenone and appearance of its effect					Average
6×10^{-8} ..	17·0	18·2	18·1	17·15	18·00	17·69
8×10^{-8} ..	10·0	11·0	10·2	11·50	10·30	10·40
10^{-7} ..	5·0	6·0	5·3	5·45	5·10	5·37
12×10^{-7} ..	3·0	2·4	3·1	2·50	2·30	2·66
14×10^{-7} ..	2·0	2·5	2·3	3·00	2·45	2·45

From Table I, it is clear that the lower the concentration of rotenone the greater is the time-lag between the administration of the rotenone and appearance of its effect. Beyond a certain concentration the time-lag between the administration of the rotenone solution and onset of its effect does not vary much. The threshold concentration appears to be about 10^{-7} with a time-lag of 5·37 minutes.

Treatment with nicotine 5×10^{-5} for three hours does not in any way modify the action of rotenone 8×10^{-8}; the rotenone effect is evident as usual. After appearance of the effect of rotenone 8×10^{-8}, the addition of 5×10^{-5} nicotine or ACH 10^{-5}, which normally causes an immediate increase in the frequency of the heart, has no effect; whereas adrenaline 5×10^{-6} induced in some cases an immediate increase in the frequency of the heart which however soon disappears, the action of rotenone again predominating. On perfusion with a mixture of nicotine 5×10^{-5} and rotenone 5×10^{-8}, an immediate increase in the frequency of the heart occurs, followed by depression, and shortly afterwards the inhibiting effect of rotenone becomes apparent. This initial acceleration is evidently due to the nicotine which is able to exert its effect on the heart during the short time-lag before rotenone begins to produce its effect on the heart.

Parathion (PATH).—Perfusion with different concentrations (10^{-6} to 5×10^{-7}) of pure parathion solution does not produce any effect on the frequency of the heart-beat; whereas on perfusion with pure parathion 10^{-6} which has been exposed to ultra-violet light for an hour, a steady increase in the frequency of the heart-beat occurs (fig. 8), the increased frequency being sustained for some hours.

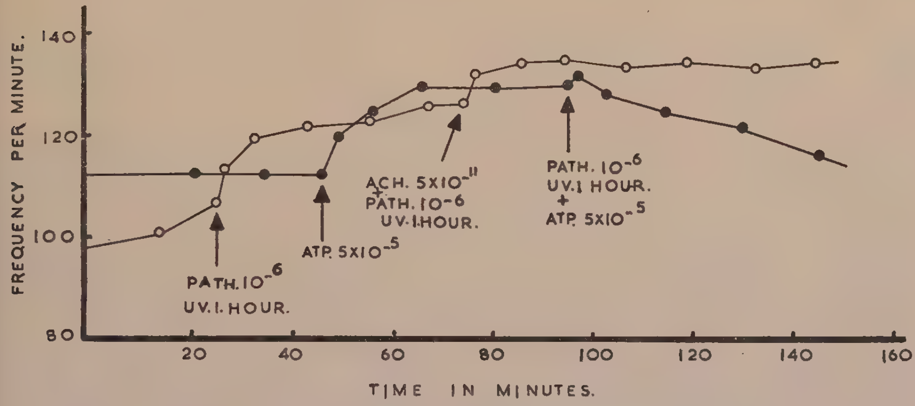


Fig. 8.—The effect of irradiated pure parathion on the frequency of the beat of the isolated heart of the cockroach, its potentiating action on a dilute solution of acetylcholine, and the blocking effect on its action by atropine.

In all the cases the amplitude of the heart-beat increases and there are occasional pauses in diastole. These effects of parathion appear to be similar to those of eserine and acetylcholine. Control experiments by exposing only the physiological solution for an hour to ultra-violet rays do not have any effect on the rate of the heart-beat.

Previous treatment with atropine 5×10^{-5} for 30 minutes blocks completely the action of irradiated pure parathion 10^{-6}. Irradiated parathion 10^{-6} is found to potentiate the action of ACH 5×10^{-11} (fig. 8) as is observed in the case of eserine (p. 209).

Paraoxon (PARA).—Paraoxon at a concentration of 3×10^{-6} does not produce any effect on the frequency of the heart-beat on perfusion but at a dilution of 15×10^{-7} an immediate increase in the rate of the heart results, with an increased amplitude which is sustained for about 20 minutes. Later a steady decline in the rate of the beat follows, with pauses in diastole at intervals. This action of paraoxon appears to be similar to that of irradiated pure parathion.

It is found that after treating the heart with paraoxon 15×10^{-7} for 30 minutes the addition of ACH 5×10^{-11} (which alone does not produce any effect on the heart) causes an increase of frequency of the heart-beat. Atropine 5×10^{-5} is found to block the action of paraoxon 15×10^{-7}.

Effect of dichlorodiphenyl-trichloroethane (DDT).—Preliminary experiments with DDT 10^{-5} suspension show that it does not produce any effect on the heart for five to seven minutes, but later produces irregular and unco-ordinated intermittent rapid and slow beating of varying amplitude. The heart-beat is interrupted by pauses at intervals either in systole or in diastole resulting in a progressive fall in the rate of the beat. Similar effects were also produced with DDT 2×10^{-5}. Previous treatment with atropine 5×10^{-5} for 30 minutes does not modify the action of DDT 10^{-5} on the cockroach heart.

Discussion and Conclusions.

Responses to autonomic drugs.

The results of the present investigation show that after paralysis of the cardiac ganglia by prolonged exposure to nicotine or by hexamethonium, ACH in low concentration still accelerates the heart. Atropine, which abolishes the "muscarine-like" actions of ACH in vertebrates, antagonises the action of low concentration of ACH on the heart. Therefore it is evident that ACH in low concentrations acts primarily on the cardiac muscle and not on the cardiac ganglia. Consequently, it is reasonable to conclude from the above results that a mechanism similar in principle to the parasympathetic system of vertebrates is involved in the working of the heart of the cockroach.

That adrenaline also acts on the muscle and not on the ganglia is apparent from the fact that neither prolonged action of nicotine nor hexamethonium, which both paralyse the cardiac ganglia, modifies its action. It is also observed that atropine, which antagonises the peripheral action of ACH, does not interfere with the action of adrenaline. Ergotamine antagonises the action of adrenaline but neither blocks the action of ACH nor is its action modified by prolonged exposure to nicotine. Therefore, it is obvious that the site of action of adrenaline and ergotamine is the same. These results show that a system corresponding in principle to the vertebrate sympathetic system is also involved in the mechanism of the heart of the cockroach. This point of view is strengthened by the statement of Elliott (1905), "A positive reaction to adrenaline is a trustworthy proof of the existence and nature of sympathetic nerves in any organ."

It has already been pointed out earlier, while discussing the prolonged action of nicotine, that the drug paralyses completely the cardiac ganglia; that nicotine acts on the ganglia is further evident from the blocking action of hexamethonium, a ganglionic blocker. From the actions of ACH, low concentration adrenaline and ergotmine after prolonged nicotine, it is clear that nicotine has no direct effect at the nerve ending or on the muscle itself. Among vertebrates also, Langley (1901) has definitely shown that nicotine stimulates the nerve-cells only and does not stimulate the nerve endings. The findings of Ellis, Thienes & Wiersma (1942) on crayfish also show that nicotine has no influence on the nerve-muscle system.

It is well established that in mammals nicotine acts on all autonomic ganglia, whether cholinergic or adrenergic. Since nicotine acts on the cardiac ganglia of the cockroach in a similar manner, it may readily be assumed that the cardiac ganglia of the cockroach are also autonomic in nature. The findings of Roeder & Roeder (1939) on the nerve cord of *Periplaneta* also support this view.

The question now arises whether the cardiac ganglia of the cockroach stimulated by nicotine are cholinergic or adrenergic or both. The antagonism exhibited between atropine and nicotine indicates undoubtedly the presence of cholinergic ganglia, since atropine is a powerful blocking agent of a cholinergic system. That cholinergic ganglia are involved in the action of nicotine and that nicotine produces most of its effect largely by stimulating ganglia which release ACH at their post-ganglionic nerve-endings is evident from the following facts: eserine is found to potentiate the action of nicotine and ACH and not that of adrenaline; the effects on the heart produced by a low concentration of nicotine are very similar to those of ACH. Further, doses of ergotamine effective against adrenaline do not detectably reduce the stimulating effect of nicotine on the heart.

The presence of adrenergic ganglia liberating an adrenaline-like substance at the post-ganglionic nerve-endings is suggested by the fact that low concentration of atropine (5×10^{-5}) does not completely block the action of ACH 10^{-3}. This effect of ACH is due to its action on the ganglia which is obvious from the fact that after blocking the peripheral action of ACH by a low concentration of atropine and the ganglia by nicotine (prolonged action), no effect is produced on the heart by ACH at high concentration. Presumably stimulation of the ganglia by ACH 10^{-3} in the presence of a low concentration of atropine is adrenergic in nature, since atropine has no influence on the peripheral effects of adrenaline. The slight increase induced by nicotine in the frequency of the heart-beat after a low concentration of atropine treatment suggests that its action is on the adrenergic ganglia. The findings of Dale (1914) support the above conclusions. He was able to demonstrate in vertebrates a stimulant action of ACH on vasomotor ganglia abolishing the depressor " muscarine-like " action with atropine, and showed that large doses of nicotine reversed this effect. The positive effect of adrenaline and nor-adrenaline on the heart also strongly favour the presence of adrenergic ganglia.

However, the possibility of high concentration ACH and nicotine acting on the heart by breaking through the barrier of low concentration atropine should not be overlooked. It is observed that high concentration of atropine completely abolishes the action of nicotine and high concentration ACH, but this does not disprove the presence of adrenergic ganglia, since atropine in high concentration in vertebrates can paralyse ganglia in addition to its action at the periphery (Marrazzi, 1939). More puzzling is the fact that the action of nicotine is not modified detectably by ergotamine. From this experiment it appears that ganglia of adrenergic nature, if present at all, can only be present in small numbers.

It is clear from these results that the nature of the cardiac ganglia of the cockroach is predominantly cholinergic and it appears that a relatively small number of adrenergic ganglia may also be present. The results also show that in many respects the responses of the cockroach heart correspond quite closely to those of mammals, apart from the reversed action of acetylcholine. As in mammals, good evidence exists in the insect for a cholinergic system liberating ACH at the nerve-endings of the post-ganglionic fibres. But only suggestive evidence could be offered for the presence of adrenergic ganglia liberating an adrenalin-like substance at the post-ganglionic fibres.

Mode and site of action of insecticides.

The response of the heart of the cockroach to pyrethrum suggests a similarity in action to that of nicotine. Further, previous treatment with pyrethrum 10^{-8} substantially reduces the normal stimulating action on the heart of nicotine 5×10^{-5}. Hence it is concluded that the site of action of nicotine and pyrethrum is the same, both acting on the cardiac ganglia causing paralysis. This conclusion is further supported by the findings of Lowenstein (1942) on isolated nerve cord of *Blatta*.

On the other hand, previous treatment with nicotine does not seem to modify the stimulating action of pyrethrum. This evidently indicates that pyrethrum, unlike nicotine, not only acts on the cardiac ganglia but also at some other site. Evidence of action by pyrethrum at the neuro-muscular junction is apparent from the fact that pyrethrum induces acceleration of the heart-beat despite paralysis of the cardiac ganglia by prolonged nicotine action. There is evidence, therefore, that pyrethrum produces its effect on the heart by acting at two different sites. This opinion is strongly supported by the findings of Ellis, Thienes & Wiersma (1942), who observed that when pyrethrum was applied to the peripheral nerve-muscle preparation of the crayfish, pronounced spontaneous contractions were produced while nicotine did not have this effect.

The action of pyrethrum on the ganglia in the present investigation may be explained as follows. On excitation of the cardiac ganglia, ACH is released at the nerve endings, and this produces the effect on the heart, but the action of pyrethrum directly at the neuro-muscular junction requires careful consideration. There are two possible ways by which pyrethrum could act. Pyrethrum is able to act directly at the nerve endings, causing a release of ACH from the bound reserves which produce the effect; the existence of ACH in the bound form in the cockroach nerve cord has been reported by Tobias, Kollros & Savit (1946). The second possibility is that perhaps pyrethrum is acting by inhibiting the cholinesterase of the tissue at both the sites. Richards & Cutkomp (1945) have shown that pyrethrum concentrate has no effect on the hydrolysis of either ACH or acetyl-β-methylcholine; and the stimulation of the heart caused by pyrethrum after prolonged exposure to nicotine in the present investigation is not sustained as with eserine but, on the contrary, soon subsides. Therefore it seems unlikely that the effect of the pyrethrum would be a result of an inhibition of cholinesterase. It appears to be much more probable that ACH is being released by pyrethrum acting on the ganglia and at the nerve endings. That ACH is involved in the actions of pyrethrum is substantiated by its potentiating action of ACH, and its actions are antagonised by atropine, a well known cholinergic blocker in vertebrates.

The results show that the heart is very sensitive to rotenone. At all concentrations the insecticide produces an inhibitory effect on the heart, characterised by irregular diastolic contractions. These results are in agreement with the findings of Krijgsman, Dresden & Berger (1950) on *Periplaneta*, Orser & Brown (1951) on the cockroach and Tischler (1935) on *Bombyx* larvae.

It is shown that the manifestations of the inhibitory effect of rotenone on the heart depends directly on the concentration of the rotenone. It is also observed that the time-lag before the appearance of the rotenone effect does not vary much after a certain concentration of the drug has been reached (Table I). Therefore, it is reasonable to conclude that a certain definite quantity of the insecticide is necessary to produce its effect on the insect heart. Rotenone seems to act as a cumulative poison, since even very dilute solutions finally result in toxic effects. It is probable that the insecticide is firmly retained in the tissue, since its action is not reversible on washing with the physiological solution. The findings of Ambrose & Haag (1938) in vertebrates also show the accumulation of the insecticide in various tissues. Strong concentration of rotenone seems neither to increase the intensity of its inhibition on the heart nor to produce more immediate effects than the weaker concentration. This shows that, perhaps after reaching the critical concentration, the entry of the insecticide into the tissue is either restricted or that any excess quantity is not able to produce further visible effects on the heart. These restrictions may be perhaps under the control of the tissue itself.

Some evidence is available with regard to the site and mode of action of rotenone, although it is not possible to draw any decisive conclusions. Rotenone is found to oppose the action of nicotine which specifically acts on the ganglia. Moreover, it is also observed that after the cardiac ganglia have been paralysed by prolonged nicotine action, rotenone still exhibits its inhibitory effect on the heart of the cockroach. This suggests, therefore, that rotenone acts both on the cardiac ganglia and on the cardiac muscle. However, Krijgsman & Krijgsman-Berger (1951), working on the isolated heart of the cockroach, put forward the view that the decrease in the rate of frequency of the heart by rotenone was mostly due to an inhibition of the ganglion cells. The inhibitory effect of rotenone on the action of ACH in contrast to its partial inhibitory effect on adrenaline suggests that rotenone is a cholinergic inhibitor. However, there appears a possibility of rotenone acting directly on the muscle and thus disturbing the metabolic activity of the cell.

It is evident from the present findings that parathion, when pure, has no influence on the isolated heart of the cockroach. It may therefore be presumed that this substance in a pure form does not inhibit cholinesterase *in vitro*. A similar situation is also recorded for mammals by Aldridge & Barnes (1952), Diggle & Gage (1951) and Payton (1953), but they report it to be a powerful inhibitor of cholinesterase *in vivo*. On the other hand, Brown (1951) suggested that parathion inhibits the cholinesterase of *Periplaneta* both *in vitro* and *in vivo*. It is highly possible that parathion contaminated with its isomers diethyl-p-nitrophenyl phosphate (paraoxon) or diethyl S-p-nitrophenyl thiophosphate, which possess anti-cholinesterase activity *in vitro* might have been employed for testing. The present studies give grounds for accepting this possibility, since perfusion with paraoxon was found to increase the rate of beat of the isolated heart of the cockroach. On the other hand, that parathion inhibits cholinesterase *in vivo* in insects is evident from the findings of Orser & Brown (1951) who observed that parathion increases the rate of the heart-beat of the insect but only after some time. Consequently it appears that even in living insects parathion does not develop an anti-cholinesterase property until it has been attacked by some metabolic system within the body of the insect. It is well known that parathion is converted by the liver to an active inhibitor of its toxicity to mammals (Aldridge & Barnes, 1952; Diggle & Gage, 1951).

It is found that pure parathion mixed with the physiological solution and exposed to ultra-violet rays for an hour, on perfusion accelerates the isolated heart of the cockroach, an effect which resembles that of eserine and ACH. Therefore it is concluded that pure parathion develops an anti-cholinesterase property after exposure to ultra-violet rays. This result is in accordance with the findings of Payton (1953). The cause for this activation is not fully understood. It is likely that parathion is being converted to one of its isomers, probably paraoxon, since the effects produced by this compound on the heart are similar in most respects to that of pure parathion exposed to ultra-violet rays.

The conclusion that irradiated parathion possesses anti-cholinesterase properties, and acts mainly at the neuro-muscular junction, is further supported by the antagonism exhibited towards it by atropine, which antagonises the "muscarine-like" action of ACH in vertebrates. Among vertebrates, also, it is presumed that organic phosphorus insecticides produce "muscarine-like" effects, which are the earliest and commonest signs of poisoning (Grob, 1950).

The effect of DDT is most erratic and is accompanied by a general decline in the rate of the heart-beat. These results differ from those of Orser & Brown (1951) on *Periplaneta*, and Davenport (1949) on *Stenopelmatus*, who did not find a significant effect of DDT on the heart.

The effects caused by the injection of DDT in the cockroach are reported by Tobias, Kollros & Savit (1946) to be similar to those due to eserine. However, in the present investigation the effect produced by DDT on the heart is not similar to that of eserine, but resembles the effect produced by high concentration of nicotine. Obviously this suggests that the action of DDT on the heart is not due to an anti-cholinesterase activity, a point of view further supported by the fact that DDT does not inhibit *in vitro* the isolated cholinesterase of insect nerves (Richards & Cutkomp, 1945). It appears to be more likely that DDT increases nerve ACH not by inhibiting the cholinesterase but by accelerating ACH liberation from the bound reserves as suggested by Tobias, Kollros & Savit (1946). But it is surprising that previous treatment with atropine, which abolishes the action of ACH, does not modify in any way the action of DDT on the isolated heart.

Summary.

The action of certain drugs and insecticides on the frequency of the beat of the isolated cockroach heart, immersed in an aerated physiological solution at 29°C., have been studied. The frequency of the heart-beat is counted by eye and the drugs applied in the physiological solution. Acetylcholine at a concentration of 5×10^{-8} to 10^{-5} causes a sustained acceleration of the heart-beat which is blocked by atropine (5×10^{-5}) and is unaltered by hexamethonium (5×10^{-5}), prolonged exposure to nicotine (5×10^{-5}) or ergotamine (3×10^{-6}). In this range of concentration ACH has a "muscarine-like" action.

Adrenaline (3×10^{-6} to 5×10^{-8}) also causes an acceleration of the heart-beat, which soon passes off. Nor-adrenaline has the same action. Nicotine, hexamethonium or atropine do not modify the action of adrenaline, but ergotamine antagonises it.

Nicotine (5×10^{-5}) produces an acceleration of the heart-beat which declines with prolonged exposure until ultimately no effect is produced on reapplication, but recovery occurs with sufficient washing. Hexamethonium antagonises the effects of low concentration of nicotine. It is concluded that nicotine acts on the cardiac ganglia. Since atropine substantially reduces the action of nicotine, it is suggested that the ganglia excited may be chiefly cholinergic.

ACH in high concentration (10^{-3}) in the presence of atropine (5×10^{-5}) has a stimulant effect which is abolished by nicotine. It is inferred that under these conditions, ACH is stimulating ganglia which may be adrenergic.

Atropine (5×10^{-5}) itself stimulates the heart somewhat, and this action is abolished by nicotine.

Eserine (5×10^{-6} to 10^{-5}) causes a sustained acceleration of the heart-beat as does ACH. The stimulant action of eserine is blocked by atropine and unaltered by nicotine. Eserine is found to potentiate the action of ACH and nicotine and not that of adrenaline.

The effects of pyrethrum are partially antagonised by low concentrations of atropine and completely by higher concentrations. Prolonged nicotine action does not modify the action of pyrethrum, but previous treatment with low concentration pyrethrum reduces substantially the effect of nicotine. It is concluded that pyrethrum acts both on the ganglia and at the neuro-muscular junction by the release of ACH and not by virtue of an anti-cholinesterase action.

Rotenone acts as a cumulative poison. The actions of ACH and nicotine are antagonised by rotenone, that of adrenaline only partially, while prolonged nicotine action does not modify the inhibitive action of rotenone.

Pure parathion has no effect on the frequency of the heart-beat, while irradiated pure parathion accelerates it and potentiates the action of ACH. Atropine abolishes the effect of irradiated pure parathion. It is suggested that, after exposure to ultra-violet rays, pure parathion is converted to some isomer which has anti-cholinesterase property.

Paraoxon was found to act on the heart in similar manner to pure parathion exposed to ultra-violet rays.

DDT causes much irregularity in the heart-beat with a decline in the rate of frequency. The effect of DDT is not modified by atropine. It appears that the action of DDT is not due to an anti-cholinesterase property.

Acknowledgements.

I am greatly indebted to Professor P. A. Buxton, C.M.G., F.R.S., for his valuable advice and encouragement. I am also grateful to Dr. W. D. M. Paton, of University College Hospital Medical School, for his helpful suggestions and criticism offered during the progress of this investigation.

References.

Aldridge, W. N. & Barnes, J. M. (1952). Some problems in assessing the toxicity of the "organo-phosphorus" insecticides towards mammals.—Nature, Lond., **169**, p. 345.

Alexandrowicz, J. S. (1926). The innervation of the heart of the cockroach (*Periplaneta orientalis*).—J. comp. Neurol., **41**, p. 291.

Ambrose, A. M. & Haag, H. B. (1938). Chronic toxicity of derris.—Industr. Engng Chem., **30**, p. 592.

Brown, A. W. A. (1951). Insect control by chemicals, p. 325.—New York, Wiley; London, Chapman & Hall.

Chadwick, L. E. & Hill, D. L. (1947). Inhibition of cholinesterase by di-isopropyl fluorophosphate, physostigmine and hexaethyl tetraphosphate in the roach.—J. Neurophysiol., **10**, p. 235.

Dale, H. H. (1914). The action of certain esters and ethers of choline and their relation to muscarine.—J. Pharmacol., **6**, p. 147.

Davenport, D. (1949). Studies in the pharmacology of the heart of the Orthopteron *Stenopelmatus*.—Physiol. Zool., **22**, p. 35.

Diggle, W. M. & Gage, J. C. (1951). Cholinesterase inhibition by parathion *in vivo*.—Nature, Lond., **168**, p. 998.

Elliott, T. R. (1905). The action of adrenalin.—J. Physiol., **32**, p. 401.

Ellis, C. H., Thienes, C. H. & Wiersma, C. A. G. (1942). The influence of certain drugs on the crustacean nerve-muscle system.—Biol. Bull., **83**, p. 334.

Grob, D. (1950). Pharmacology and toxicology of certain organic phosphorus insecticides. Toxicology.—J. Amer. med. Ass., **144**, p. 105.

Hamilton, H. L. (1939). The action of acetylcholine, atropine and nicotine on the heart of the grasshopper (*Melanoplus differentialis*).—J. cell. comp. Physiol., **13**, p. 91.

Hopf, H. S. (1952). Studies in the mode of action of insecticides. I. Injection experiments on the role of cholinesterase inhibition.—Ann. appl. Biol., **39**, p. 193.

Imms, A. D. (1948). A general text book of entomology.—7th edn., 727 pp. London, Methuen.

Krijgsman, B. J., Dresden, D. & Berger, N. E. (1950). The action of rotenone and tetraethyl pyrophosphate on the isolated heart of the cockroach.—Bull. ent. Res., **41**, p. 141.

Krijgsman, B. J. & Krijgsman-Berger, N. E. (1951). Physiological investigations into the heart function of arthropods. The heart of *Periplaneta americana*.—Bull. ent. Res., **42**, p. 143.

Langley, J. M. (1901). On the stimulation and paralysis of nerve cells and of nerve endings. Part I.—J. Physiol., **27**, p. 224.

Lord, K. A. & Potter, C. (1951). Studies on the mechanism of insecticidal action of organo-phosphorus compounds with particular reference to their anti-esterase activity.—Ann. appl. Biol., **38**, p. 495.

Lowenstein, O. (1942). A method of physiological assay of pyrethrum extracts. —Nature, Lond., **150**, p. 760.

McIndoo, N. E. & Smithson, –. (1945). Innervation of insect hearts.—J. comp. Neurol., **83**, p. 141.

MARRAZZI, A. S. (1939). Electrical studies on pharmacology of autonomic synapses; action of sympathomimetic drug (epinephrine) on sympathetic ganglia.—J. Pharmacol., **65**, p. 395.

MEANS jr., O. W. (1942). Cholinesterase activity of tissues of adult *Melanoplus differentialis* (Orthoptera, Acrididae).—J. cell. comp. Physiol., **20**, p. 319.

ORSER, W. B. & BROWN, A. W. A. (1951). The effect of insecticides on the heartbeat of *Periplaneta*.—Canad. J. Zool., **29**, p. 54.

PAYTON, J. (1953). "Parathion" and ultra-violet light.—Nature, Lond., **171**, p. 355.

PRINGLE, J. W. S. (1938). Proprioception in insects. I. A new type of mechanical receptor from the palps of the cockroach.—J. exp. Biol., **15**, p. 101.

PROSSER, C. L. (1940). Action potentials in the nervous system of the crayfish. Effects of drugs and salts upon synaptic transmission.—J. cell. comp. Physiol., **16**, p. 25.

PROSSER, C. L. (1942). An analysis of the action of acetylcholine on hearts, particularly in Arthropods.—Biol. Bull., **83**, p. 145.

RICHARDS jr., A. G. & CUTKOMP, L. K. (1945). The cholinesterase of insect nerves.—J. cell. comp. Physiol., **26**, p. 57.

ROEDER, K. D. & ROEDER, S. (1939). Electrical activity in the isolated ventral nerve cord of the cockroach, I.—J. cell. comp. Physiol., **14**, p. 1.

TISCHLER, N. (1935). Studies on how derris kills insects.—J. econ. Ent., **28**, p. 215.

TOBIAS, J. M., KOLLROS, J. J. & SAVIT, J. (1946). Acetylcholine and related substances in the cockroach, fly and crayfish and the effect of DDT.—J. cell. comp. Physiol., **28**, p. 159.

PSEUDOTHERAPTUS WAYI, A NEW GENUS AND SPECIES OF COREID (HEMIPTERA) INJURIOUS TO COCONUTS IN EAST AFRICA.

By E. S. Brown
Commonwealth Institute of Entomology.

The recent discovery by Way (1951, 1953) that "early nutfall" or "gummosis" of coconuts in East Africa is caused by a Coreid bug has necessitated this taxonomic study; first, to find out whether the insect is specifically distinct from previously described species, and secondly, because minor differences, requiring closer study, have been described between examples collected in Zanzibar, Pemba and the East African mainland.

The bug was at first referred to the genus *Theraptus* Stål, and has appeared as such in the literature over the past two or three years. This attribution was correct according to the current conception of this genus, because the coconut pest was obviously congeneric with the species known as *Theraptus devastans* (Dist.), from the Belgian Congo. The latter had been described by Distant

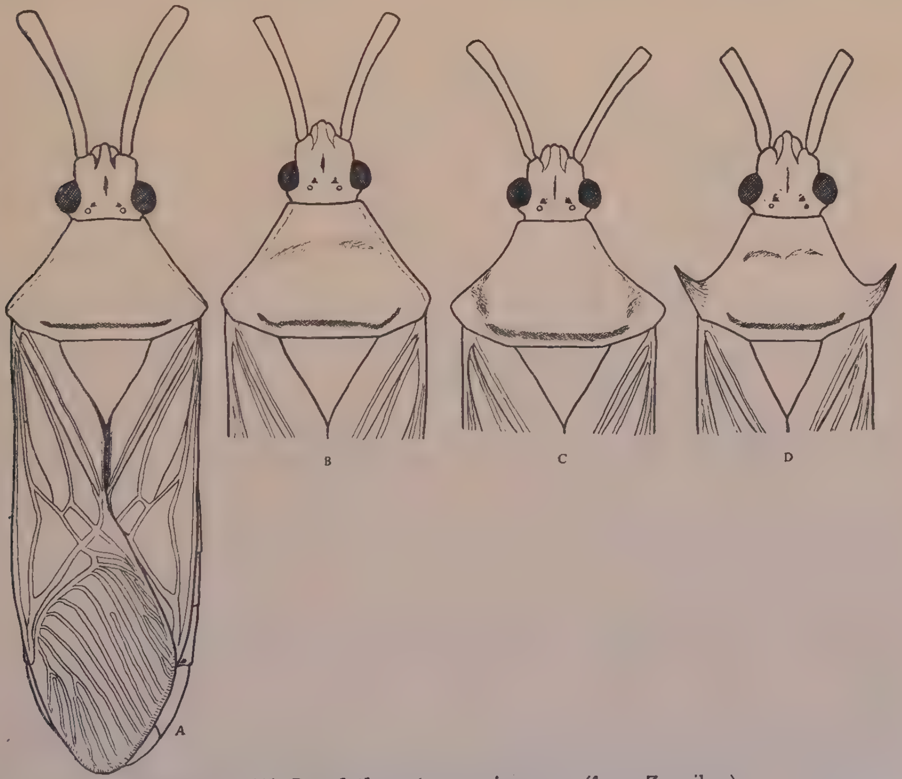


Fig. 1.—(A) *Pseudotheraptus wayi*, sp. n. (from Zanzibar); (B) *Ps. devastans* (Dist.); (C) *Ps. ugandae*, sp. n.; (D) *Plinachtus spinosus* Stål. (× 8).

(1917) in *Pendulinus* Thunberg, near to *P. carmelita* (Burm.); it was for the latter species, however, that Stål had earlier (1859) raised the genus *Theraptus*, and although the same author later (1873) reduced it to a subgenus, it has since been raised again to generic rank by China (1934), who included both *carmelita* and *devastans* in the genus. Although more recently Blöte (1935) reduced it to a subgenus of *Dasynus* Burm., there is little doubt as to its generic status.

A taxonomic study of species placed in *Theraptus* and certain related genera, however, has shown *devastans* to be generically distinct from *Theraptus carmelita* (the type species), but congeneric with the species attacking coconuts in East Africa and with another, undescribed species from Uganda. This necessitates the erection of a new genus, which is described below under the name *Pseudotheraptus*, a name chosen to indicate a certain superficial resemblance to *Theraptus* and to avoid some of the confusion which may result from the coconut pest having been widely referred to as "*Theraptus* sp." in recent years.

Pseudotheraptus, gen. n.

Medium-sized Coreids in general appearance resembling *Theraptus*; fawn or reddish-brown in colour with the membrane blackish.

Head porrect, extending well forward in between the antenniferous tubercles, the latter separated from each other by a distance about equal to their width; a well-marked median longitudinal impression on the vertex between the eyes; distance between the antennal socket and the anterior margin of the eye, seen in side view, about half the width of an eye. Bucculae long; in side view almost their entire length lying in front of a line running through the anterior margin of the eye and perpendicular to the lower margin of the head (fig. 2, A & B).

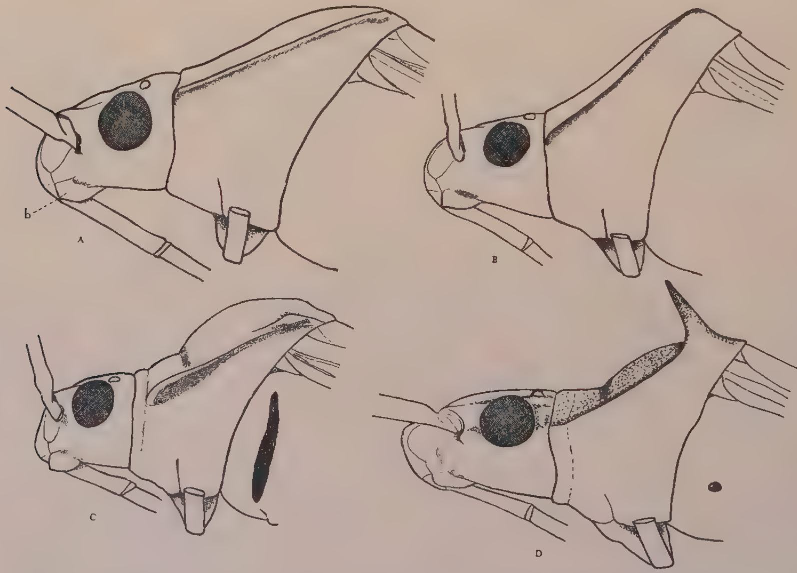


Fig. 2.—Head and thorax, from left side. (A) *Pseudotheraptus wayi*, sp. n.; (B) *Ps. ugandae*, sp. n.; (C) *Theraptus carmelita* (Burm.); (D) *Plinachtus spinosus* Stål; *b*, buccula. (× 10).

Antennae long, about equal to or slightly shorter than the combined length of head and body; the 1st, 2nd or 4th segment longest, the 3rd segment always distinctly shorter than the others; 1st segment conspicuously thicker distally than the other segments.

Pronotum without a collar anteriorly, the lateral carina reaching the anterior margin; with only a feebly developed transverse impression behind the anterior callus, the latter being scarcely evident; humeral angles obtusely or right-angled and feebly raised.

Metapleura, and sometimes mesopleura also, with a round black spot in the middle, usually raised and shining (fig. 8, E; fig. 15); peritreme of thoracic scent gland with posterior arm long and pointed (fig. 15). Mesosternum with slight median furrow.

Scutellum acutely pointed at apex, slightly broader across basal angles than the median length, and relatively broader in females than in males.

Corium with cell *m-cu* parallel-sided, almost rectangular (fig. 13, A–C).

Rostrum of somewhat variable length, reaching at least the posterior margin of the middle acetabula and sometimes beyond the posterior acetabula; 4th segment usually longest, 1st and 2nd subequal, 3rd shortest.

Pygophore (9th abdominal segment) of male with posterior margin emarginate in the centre, and a flattened, characteristically sculptured lateral process on each side produced forwards along the side of the cavity of the pygophore (fig. 3; fig. 9, A & B); the latter cavity without a transverse septum separating a posterior from an anterior compartment (fig. 10, D–F), but with a trough in the floor of the anterior part (in which the aedeagus is situated) bounded posteriorly by a slight transverse ridge (fig. 10, A). Parameres more or less straight (fig. 14, A & B).

Seventh abdominal sternum of female with median cleft extending slightly beyond the middle (fig. 11, A–C); margin of transverse fold slightly sinuate, not or only slightly angled in the middle, and almost concealed by the sternum of the 6th segment; 2nd valvula * distinctly chitinised at the tip (fig. 5).

Type species: *Pseudotheraptus wayi*, sp. n.

The relationship of *Pseudotheraptus* to allied genera is discussed later (p. 229).

Pseudotheraptus wayi, sp. n.

Colour brownish testaceous, often (particularly in dried specimens) with a reddish suffusion, especially towards the apex of the corium and sometimes of the femora; sometimes the colour dorsally is darker brownish, without a reddish tinge. Head, pronotum, scutellum and hemelytra with rather thickly distributed reddish brown punctures; veins of hemelytra and lateral carinae of pronotum paler, whitish or yellowish; membrane and hind wings smoky black, the latter with a purple iridescence by reflected light. Tibiae pinkish red. Antennae with three basal segments reddish, distal half of 4th brownish with the extreme tip usually pale. Eyes and ocelli reddish pink. Upper surface of abdomen orange to cinnamon red. Underside paler, whitish testaceous, greenish in fresh specimens, with punctures concolorous or faintly pinkish; a raised, circular, shining black spot on the metapleuron.

Head shorter than the pronotum as 19:29. Ocelli slightly nearer to the inner margins of the eyes than to the middle line. Bucculae deepest and slightly acutely pointed anteriorly (fig. 2, A). Tylus porrect, protruding well forward between the antennal tubercles.

Pronotum broader than long as 58:40, with sides straight or slightly concave, the lateral carinae approximately right-angled; posterior margin convex with the median portion across the base of the scutellum straight. A very feebly developed transverse impression behind the anterior callus, and a stronger one just inside the posterior margin. Humeral angles not conspicuous, approximately right-angled (fig. 1, A). Scent gland with posterior lobe of peritreme as long as the aperture (fig. 15).

---

* See fig. 4; the nomenclature adopted for the parts of the female genitalia, and the numbering of the segments, is that given by Snodgrass (1933).

Scutellum with the apex pointed, and the basal width greater than the median length as 31:27 (males) or 41:33 (females).

Hemelytra with cell *m-cu* nearly rectangular, parallel-sided (fig. 13, A).

Antennae long, in males and females respectively slightly longer and slightly shorter than the combined length of head and body; the ratios of segments 1–4 as 50:50:34:45. Basal segment conspicuously thickened towards apex (fig. 12, B).

Rostrum reaching at least the middle of the posterior acetabulum, and sometimes slightly beyond it; ratio of segments 1–4 as 44:43:30:49.

Pygophore of male characteristically shaped (fig. 6, A; fig. 7, A & F; fig. 9, A; fig. 10, A); median emargination deep and narrow, with lateral processes well developed, flattened and rounded or obliquely truncate apically (fig. 3). Parameres obliquely truncate apically (fig. 14, A).

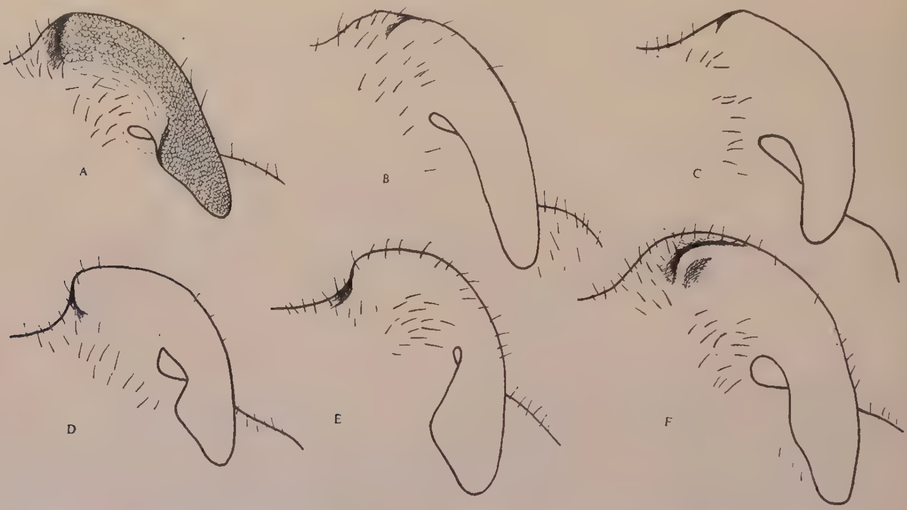


Fig. 3.—*Pseudotheraptus wayi*, sp. n. Lateral process of the left side of pygophore of male, viewed from above and slightly from inner side. The fine sculpture of the integument has been shown in (A) but omitted in the others. (A) Specimen from Pemba; (B, C) from Zanzibar; (D, E) from Tanganyika mainland (Dar-es-Salaam and Mbagalla, respectively); (F) from Kenya mainland. (× 45).

Female with chitinised apex of second valvula produced into a prominent, rounded knob (fig. 5, A).

Length, 12–13 mm. (males), 14–15·5 mm. (females); width across elytra, 4–4·5 mm. (males), 4·5–5·0 mm. (females).

Distribution.

Zanzibar: holotype (male), 1950 (*M. J. Way*); allotype (female), 1951 (*M. J. Way*); 5 paratypes and numerous other specimens (*M. J. Way* and *F. L. Vanderplank*); all in British Museum (Natural History).

Pemba: x.1951, several (*M. J. Way*); xi–xii.1951, on cocoa fruit (*G. Wilkinson*); other specimens (*F. L. Vanderplank*).

Kenya (mainland): Gazi, ix–x.1951 and Kilifi, vii.1942 (*R. Le Pelley*). Kilifi is 40 miles north, and Gazi to the south of Mombasa. The single example from Kilifi was taken on *Anacardium occidentale*, while all those from Gazi were reared on coconut.

Tanganyika: Mafia Is., xi.1951, 1 ♂, 3 ♀♀ (*M. J. Way*). Localities on the mainland (coll. *G. Swaine*): Dar-es-Salaam, 3.ix.1953 and 1954, on coconut; Mingoyo, 5.ix.1953, on fruit of *Anacardium occidentale*; Mchinga, 7.ix.1953, on fruit of *A. occidentale*; Tanga, several specimens (*F. L. Vanderplank*).

Local variation.—Attention has been given to material collected on the mainland and on the different islands, to find out if the populations are identical, or whether there is variation of specific or subspecific value.

It is clear from these investigations that all populations studied are conspecific, and also that there are insufficient differences, with the limited material available, for separation into subspecies. Variation has, however, been found in the shape of the lateral processes of the pygophore of the male. In males from Zanzibar (fig. 3, B & C) the process is more or less parallel-sided and evenly rounded at the tip, and in the single male from Mafia Island it is similar; in those from the Tanganyika mainland (fig. 3, D & E) it is strongly constricted basally and obliquely tapered apically; in specimens from Pemba (fig. 3, A) and one from Kenya mainland (fig. 3, F), the condition is more or less intermediate. The number of examples examined, however, is very small, but if enough material becomes available to apply the 75 per cent. rule for consistency in the different areas, the erection of geographical subspecies might be justified.

There is also some variation in colour, examples from Zanzibar and Kenya being paler and more reddish, while those examined from Pemba are more greyish and much darker; the four examples from Mafia Island approach those from Pemba. However, one may find dark examples from Zanzibar, and Dr. F. L. Vanderplank informs me that considerable colour-range may occur in the same brood, according to the food-plant on which they have been reared. Colour is not therefore likely to prove a reliable taxonomic character.

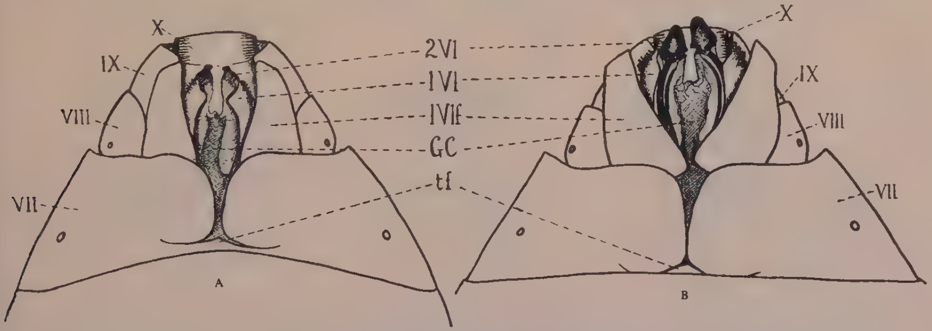


Fig. 4.—Female genitalia in ventral view, with first valvifers (1Vlf) parted to show internal structures. (A) *Pseudotheraptus devastans* (Dist.); (B) *Ps. wayi*, sp. n. In (B) the 1st valvulae (1Vl) have been drawn further aside to show the chitinised supporting rods of the 2nd valvulae (2Vl). Other lettering: GC, genital chamber; tf, transverse fold in the 7th sternum; VII–X, 7th to 10th abdominal segments (numbered after Snodgrass, 1933). (× 13).

Some breeding experiments carried out in Zanzibar (Tait, 1954) are not inconsistent with the views expressed above. She cross-bred in various ways examples collected in Zanzibar, Pemba and Tanganyika. Selfing of those from Zanzibar produced eggs which were 100 per cent. fertile, and of those from Tanganyika, eggs which were 94·5 per cent. fertile. When parents of different origin were crossed, the fertility of eggs of the first generation varied between

70·5 and 100 per cent. and when the F_1 were themselves selfed, fertility sank to a range of 33·3–68·4 per cent. in different cases; it is of interest that the lowest fertility resulted from Zanzibar and Tanganyika grandparents, which show the maximum difference in the lateral processes of the male pygophore. There thus appear to be genetic differences of varying importance in the different populations, but it would be necessary to repeat these experiments on a larger scale to draw firm conclusions as to the details.

Pseudotheraptus devastans (Distant).

Pendulinus devastans Distant (1917).

Theraptus devastans China (1934).

Theraptus devastans Schouteden (1938).

In general external form and coloration this species is almost inseparable from *Ps. wayi.*

The antennae (fig. 12, A) are about equal in length to the head and body combined; the 1st segment is slightly less inflated in the distal half, and the length ratios of the segments are different, the 1st being shorter than both the 2nd and the 4th, which are subequal; the ratios of segments 1–4 are as 38:46:30:48.

Pronotum (fig. 1, B) with length:width ratio as 2:3; the lateral carinae scarcely paler than the disc, almost or quite concolorous.

Scutellum relatively longer than in *wayi*, the basal width only slightly greater than the median length; the length:width ratio is as 26:27 in males, and 28:31 in females.

In the genitalia it differs sharply from *wayi.* The male pygophore (fig. 6, B; fig. 7, B & G; fig. 9, B) is larger and has the median emargination in the posterior border shallower, and the lateral processes less prominent externally; the parameres (fig. 14, B) are gently tapered apically, and not obliquely truncate. The chitinised apex of the 2nd valvula of the female (fig. 5, B) is without a distal inflation.

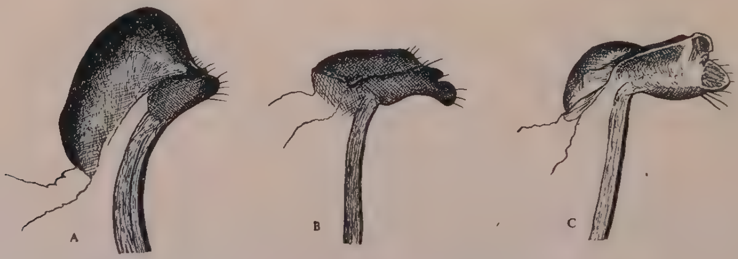


Fig. 5.—Chitinised apex of second valvula of right side of female, inner view. (A) *Pseudotheraptus wayi*, sp. n.; (B) *Ps. devastans* (Dist.); (C) *Ps. ugandae*, sp. n. (× 45).

Length, 12 mm. (male), 13 mm. (female); width across elytra, 4 mm. (male), 4·5 mm. (female).

Distribution.

In addition to the earlier records from the Belgian Congo (Distant, 1917; Schouteden, 1938) the following material has been examined in the collection of the British Museum (Natural History).

Gold Coast: Aburi, 1912–13, 2 ♂♂, 2 ♀♀ (*W. H. Patterson*); Bompata, Ashanti, 1 ♀ (*H. E. Evans*).

Nigeria: Ibadan, 29.vii.1935, 2 ♀♀, on *Manihot utilissima* (*F. D. Golding*).

CAMEROONS: D'Ja Posten, lat. 3·15 N., long. 13·30 E., 15.v–1.vii.1936, 2 ♂♂ (*F. G. Merfield*).

The species thus appears to have a wide range across central and western tropical Africa. There is insufficient material to analyse the question of subspeciation. The Gold Coast specimens have the shoulders of the pronotum suffused with a reddish colour.

Pseudotheraptus ugandae, sp. n.

In general coloration and appearance this species is similar to *Ps. wayi* and *Ps. devastans*, and the description of the former given above might equally apply except for the following differences, which separate it from both species much more sharply than they differ from one another:—

1. The pronotum is relatively broader (length : width as 38 : 63), and differently shaped; the lateral margins are concave (fig. 1, C); the humeral angles are more pronounced and turned upwards, so that the shoulders are more pronounced in lateral view (fig. 2, B), and the disc appears more hollowed when viewed from above or behind.
2. The lateral carinae and humeral angles are distinctly reddish, darker than the disc rather than paler or concolorous as in the other species.
3. The distal part of the corium is more distinctly reddish.
4. There is a black spot on the mesopleura as well as the metapleura.
5. The antennae are testaceous to brownish rather than reddish; the terminal segment is darker and thicker (fig. 12, C).
6. The antennae are shorter, and the ratios of the segments differ from those of *devastans*, the 1st being longer than the 2nd and the 4th, and the 2nd slightly longer than the 4th; the ratios of segments 1–4 are as 42 : 39 : 28 : 37.

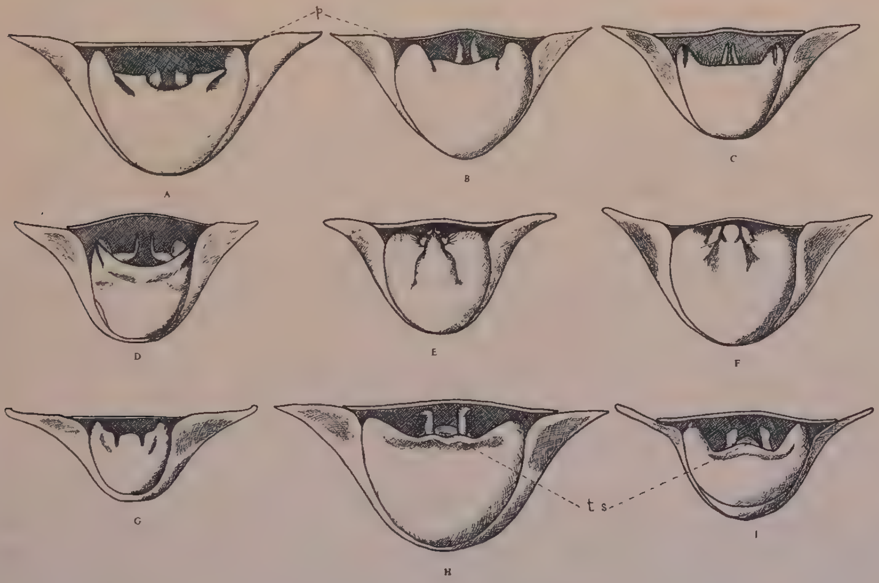


Fig. 6.—Rear view of male abdomen. (A) *Pseudotheraptus wayi*, sp. n.; (B) *Ps. devastans* (Dist.); (C) *Ps. ugandae*, sp. n.; (D) *Plinachtus spinosus* Stål; (E) *Theraptus carmelita* Stål; (F) *Th. maculatus* Schout.; (G) *Dasynus nigromarginatus* (Dist.); (H) *D. coccocinctus* (Burm.); (I) *Amblypelta cocophaga* China. *p*, parameres; *t.s.*, transverse septum. (× 10).

7. The 1st and 4th rostral segments are subequal, whereas the 4th is longer in *wayi* and *devastans*; the ratios of segments 1–4 are as 37:35:20:38.

8. The pygophore of the male is differently shaped; the median emargination in rear view is broader and shallower, the lateral processes being nearer the outer margins (fig. 6, C), and presenting a different appearance in lateral view (fig. 7, H). The single male specimen has not been dissected, and the parameres have not been figured.

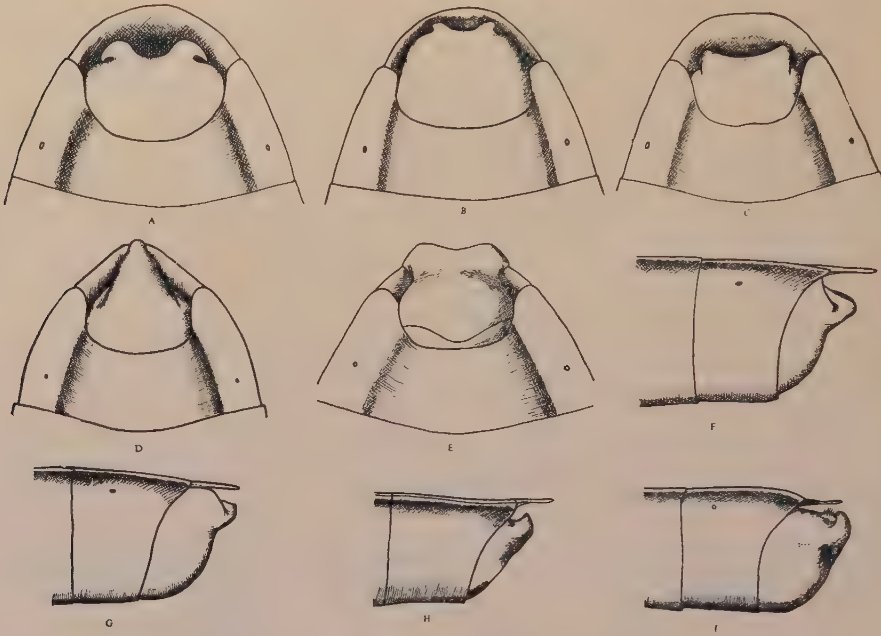


Fig. 7.—Underside (A–E) and lateral (F–I) aspects of tip of male abdomen. (A, F) *Pseudotheraptus wayi*, sp. n.; (B, G) *Ps. devastans* (Dist.); (C, H) *Ps. ugandae*, sp. n.; (D, I) *Theraptus carmelita* (Burm.); (E) *Plinachtus spinosus* Stål. (× 10).

9. The female has the first valvifer somewhat obliquely truncate (fig. 11, C), and the chitinised apex of the 2nd valvula is differently shaped (fig. 5, C).

10. The scutellum is relatively broader than in *Ps. devastans*; the ratio length: width is as 25:30 in the male and 23:29 in the female.

Length, 12 mm. (male), 13 mm. (female); width across elytra, 4 mm. (male), 4·5 mm. (female).

Distribution.

UGANDA: Tero Forest, vii.1912, 1 ♂ (holotype), 1 ♀ (allotype) (*C. C. Gowdey*). Both specimens are in the collection of the British Museum (Natural History).

The Tero Forest borders the River Kagera, which forms the boundary between Uganda and Tanganyika on the west side of Lake Victoria, at about 3,700 ft. The forest is close and swampy during the rains, and has some affinity with the Congo forest in which *Ps. devastans* occurs, although distinct and topographically isolated from it. It is also isolated from the East African coast, where *Ps. wayi* occurs, by a tract of steppe-like country.

Key to the species of *Pseudotheraptus*.

1. Humeral angles of the pronotum more strongly developed (fig. 1, C), and elevated so that the shoulders are more pronounced in lateral view (fig. 2, B). Lateral carinae of pronotum reddish, darker than the disc. A black spot on the mesopleura and metapleura. Rostrum with 1st and 4th segments subequal. Posterior margin of pygophore of male, in rear view, with median emargination broad and shallow, and the lateral processes erect and approximated to the lateral margin (fig. 6, C). Female with 1st valvifer obliquely truncate apically (fig. 11, C), and chitinised apex of 2nd valvula as in fig. 5, C. (Uganda) ... *ugandae*, sp. n.

   Humeral angles much less strongly developed (fig. 1, A & B), and shoulders not conspicuously raised in lateral view (fig. 2, A). Lateral carinae whitish or yellowish, paler than or concolorous with the disc. A black spot on the metapleura only (fig. 8, E). Rostrum with 4th segment 12–15 per cent. longer than the 1st. Pygophore of male of different form. Female with 1st valvifer more squarely truncate apically (fig. 11, A & B), and 2nd valvula of different form 2

2. 1st and 2nd antennal segments subequal, both longer than the 4th. 2nd rostral segment subequal to the 1st, both shorter than the 4th. Lateral carina of pronotum usually distinctly paler than the disc, whitish. Pygophore of male smaller, with median emargination of posterior border, seen from behind and below, deeper, and lateral processes more conspicuous (fig. 6, A; fig. 7, A & F). Parameres obliquely truncate apically (fig. 14, A). Chitinised apex of 2nd valvula of female with prominent, rounded knob (fig. 5, A). Coast of tropical East Africa, and islands of Zanzibar, Pemba and Mafia) .... *wayi*, sp. n.

   2nd and 4th antennal segments subequal, both longer than the 1st. 2nd rostral segment usually longer than the 1st and subequal to the 4th. Lateral carina of pronotum usually fawn-coloured, concolorous with the disc or only slightly paler. Pygophore of male larger, with median emargination shallower and lateral processes less pronounced (fig. 6, B; fig. 7, B & G). Parameres gently tapered apically (fig. 14, B). Chitinised apex of 2nd valvula of female as in fig. 5, B, without a prominent, rounded knob. (Belgian Congo, Nigeria, Gold Coast, Cameroons) .... *devastans* (Dist.).

Since *Pseudotheraptus* has affinities with two tribes of the subfamily COREINAE, namely the Dasynini and Gonocerini, the genera which concern us in each tribe will be considered separately below.

Tribe DASYNINI Schouteden 1938.

(= Div. *Pendulinaria* Stål 1873; = Div. *Dasynaria* Bergroth 1913; = Subfamily *Pendulinidae* Lethierry & Severin 1894).

Theraptus being a genus in this tribe, and *Pseudotheraptus* having been originally placed in *Theraptus*, it was with the genera of this tribe that it was first compared. The most important of these from the point of view of the present study are *Galaesus* Dall., *Theraptus* Stål, *Dasynus* Burm., and *Amblypelta* Stål. The type species and most others in these genera have certain features in common distinguishing them from *Pseudotheraptus*:

(1) The 1st antennal segment is not swollen apically (fig. 12, E–G).

(2) Cell *m-cu* of the hemelytra is usually divergent posteriorly and not parallel-sided (fig. 13).
(3) The circular, shining, raised black spot on the metapleuron is missing, although there may be other black markings on the underside (*e.g.*, fig. 8).

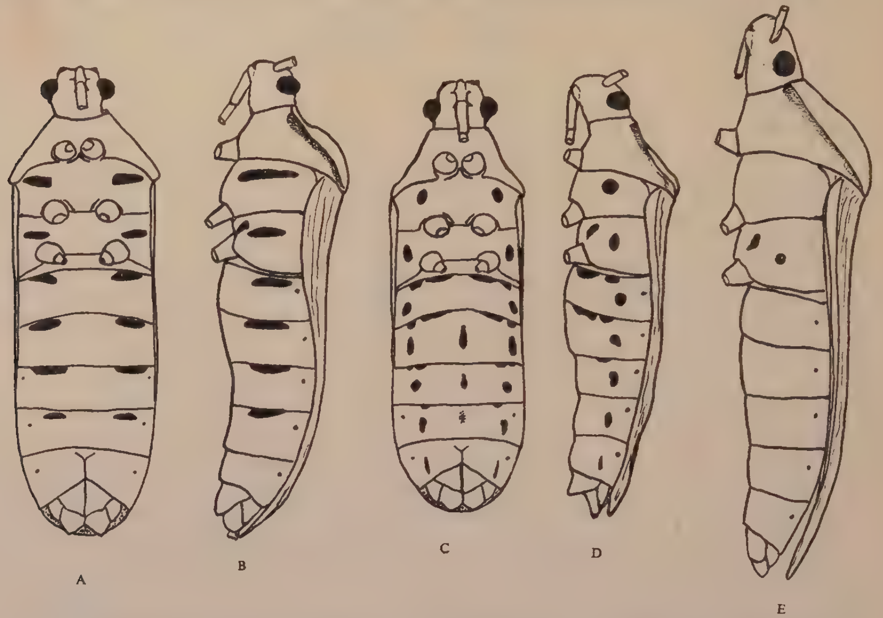


Fig. 8.—*Theraptus carmelita* (Burm.): (A) underside; (B) lateral view. *Th. maculatus* Schout.: (C) underside; (D) lateral view. *Pseudotheraptus wayi*, sp. n.: (E) lateral view. All females. (× 5).

(4) The pygophore of the male differs in important characteristics; it lacks the median emargination in the posterior border and the tongue-like lateral processes found in *Pseudotheraptus*, and the cavity has a raised transverse septum dividing it into a posterior and an anterior chamber (figs. 6, 7, 9, 10).
(5) The 7th sternum of the female has the median cleft shorter, not or scarcely reaching the centre of the segment, and the transverse fold in the segment is more or less distinctly angulate in the centre (fig. 11).

This last feature was used by Stål (1873) to distinguish his Divisions *Pendulinaria* and *Gonoceraria* (equivalent to the Tribes Dasynini and Gonocerini of Schouteden (1938)), in a couplet of his key, of which the following is a literal translation:

> Fold of the sixth[1] ventral segment of females produced into an obtuse or very obtuse angle in the middle; spiracles placed distinctly in front of the middle of the segments .... Div. *Pendulinaria* Stål
>
> Fold of the sixth ventral segment of females appreciably curved backwards and situated very close to the base of the segment, sometimes concealed beneath the apical margin of the fifth[2] segment; scutellum usually equilateral; spiracles equally or nearly equally distant from the base and apex of the ventral segments .... Div. *Gonoceraria* Stål (and Div. *Corearia* Stål).

As regards the form and position of the ventral fold of the 7th segment (6th of Stål), *Pseudotheraptus* occupies an intermediate position between the two tribes, for the fold is slightly sinuate, and only slightly angulate in the middle; a comparison of the condition with that in the Gonocerine genus *Plinachtus* on the one hand, and with various Dasynine genera on the other hand (fig. 11) will make this clear; the fold in *Pseudotheraptus* is often nearly concealed by the 6th sternum, although there is variation in this. For these, and other reasons, discussed later (p. 237), *Pseudotheraptus* shows some affinity with the Tribe Gonocerini, and may be regarded as annectent between the two Tribes.

---

[1], [2] These are the seventh and sixth segments respectively according to Snodgrass (1933), and are so regarded elsewhere in this paper.

Theraptus Stål 1859.

Pseudotheraptus differs from *Theraptus carmelita* (Burm.), the type species of its genus, in the absence of a pronotal collar and of a pronounced transverse impression behind the anterior callus, the latter being much less marked. *Theraptus* has the head much shorter and less porrect, the snout being more strongly flexed downwards and scarcely extending forwards between the antennal tubercles (fig. 2, C); the distance between the antennal socket and the anterior margin of the eye is only about $\frac{1}{4}$ the width of the eye, seen in lateral view. The bucculae in *Theraptus* are shorter, and approximately bisected by a line through the anterior margin of the eye and perpendicular to the lower margin of the head (compare this with the condition in *Pseudotheraptus*, fig. 2). The antennae are longer and more slender in *Theraptus*, especially the 1st segment, which in *Th. carmelita* is longer than the 2nd (fig. 12, E). The pygophore of the male *Theraptus* is laterally compressed and has a well-developed median lobe and reduced lateral lobes (fig. 6, E; fig. 7, D & I; fig. 9, C); and the cavity has a transverse septum separating posterior and anterior compartments (fig. 9, C). The female has the 1st valvifers strongly tapered apically and the 7th sternum has the cleft much shorter and the transverse fold short and sharply angled in the centre (fig. 11, E). There is a difference also in cell *m-cu* of the hemelytra,

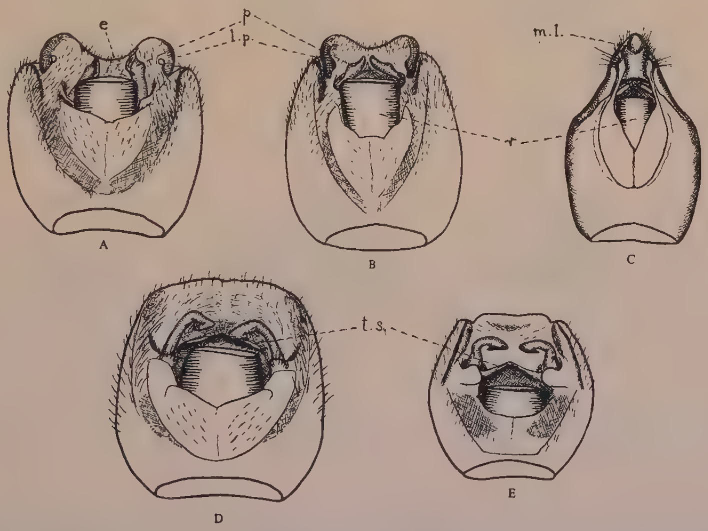


Fig. 9.—Pygophore of male, dissected out and seen in dorsal view. (A) *Pseudotheraptus wayi*, sp. n. (from Zanzibar); (B) *Ps. devastans* (Dist.); (C) *Theraptus carmelita* (Burm.); (D) *Dasynus coccocinctus* (Burm.); (E) *Amblypelta cocophaga* China. *e*, median emargination in posterior border; *l.p.*, lateral processes; *m.l.*, median lobe; *p*, parameres; *r*, rectum; *t.s.*, transverse septum. (× 13).

which is slightly divergent posteriorly in *Theraptus* instead of parallel-sided (fig. 13, F). The posterior arm of the peritreme of the scent-gland, which in *Pseudotheraptus* is long (fig. 15), is very short in *Theraptus*. The shining, raised black spot on the thoracic pleura also separates *Pseudotheraptus* from *Theraptus* which, however, has other more extensive black markings on the underside (fig. 8).

Since Stål's erection of the genus, four additional species have been placed in it: *Th. devastans* and *Th. nigromarginatus* were described by Distant (1917) in the genus *Pendulinus*, but he considered them to be most nearly related to *carmelita* which he placed in the same genus, and later China (1934), as stated above, included them all in *Theraptus*; the other two species are *Th. distanti* and *Th. maculatus* described by Schouteden (1938). The types of all four species have been examined, Distant's types being in the British Museum (Natural History), and Schouteden's being lent from the Congo Museum through the kindness of Mr. P. Basilewsky. Of these four species, *Th. devastans* is here transferred to the new genus *Pseudotheraptus*; *nigromarginatus* is clearly generically distinct from both *carmelita* and *devastans*, differing from the former in the porrect head, absence of pronotal collar and of transverse furrow behind the anterior pronotal callus, and in the differently shaped pygophore of the male (fig. 6, G; fig. 10, F), and from *Pseudotheraptus* in the slender 1st antennal segment, in the presence of a transverse septum and absence of tongue-like lateral processes in the male pygophore, and the deeply angulate emargination of the posterior border of 7th abdominal sternum of the female and the distinctly angulate transverse fold (fig. 11, F); it is best placed provisionally in *Dasynus*, although in the structure of the male pygophore and parameres (fig. 14, F) it bears some resemblance to *Galaesus*; it requires further study.

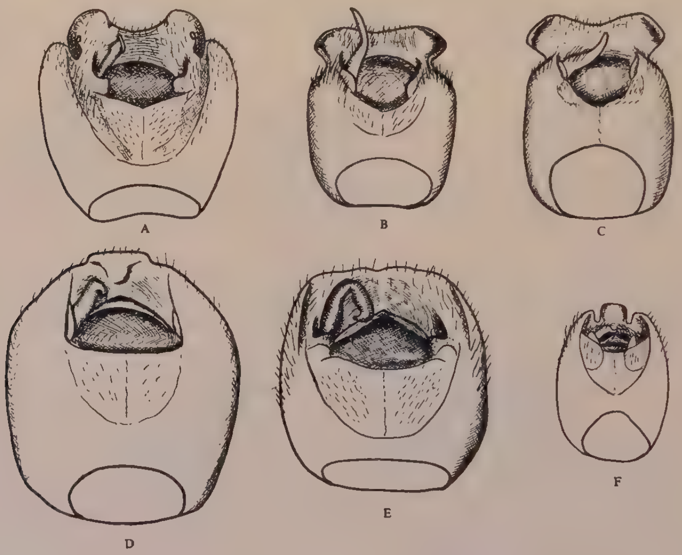


Fig. 10.—Pygophore of male in dorsal view, with rectum and left paramere removed. (A) *Pseudotheraptus wayi*, sp. n.; (B) *Plinachtus spinosus* Stål; (C) *Pl. pugionatus* Stål; (D) *Galaesus hasticornis* (Thnb.); (E) *Dasynus coccocinctus* (Burm.); (F) *D. nigromarginatus* (Dist.). See fig. 9 for names of parts. (× 13).

Of Schouteden's two species, *distanti* is clearly conspecific with *nigromarginatus*; in his description of *distanti* he mentions black markings on the head in front of and behind the eye, which are absent from the original description of *nigromarginatus*; but although Distant did not mention them, they are present in the type, although very faint, and are present to an intermediate extent in examples from other localities. The ivory white underside of the type of *distanti* is likewise a character found to varying extents in some examples of *nigromarginatus*, while the external anatomy of the male and female genital segments is identical. In addition to the original record from Natal, and of Schouteden's from the Belgian Congo, *nigromarginatus* is here recorded also from the following localities:

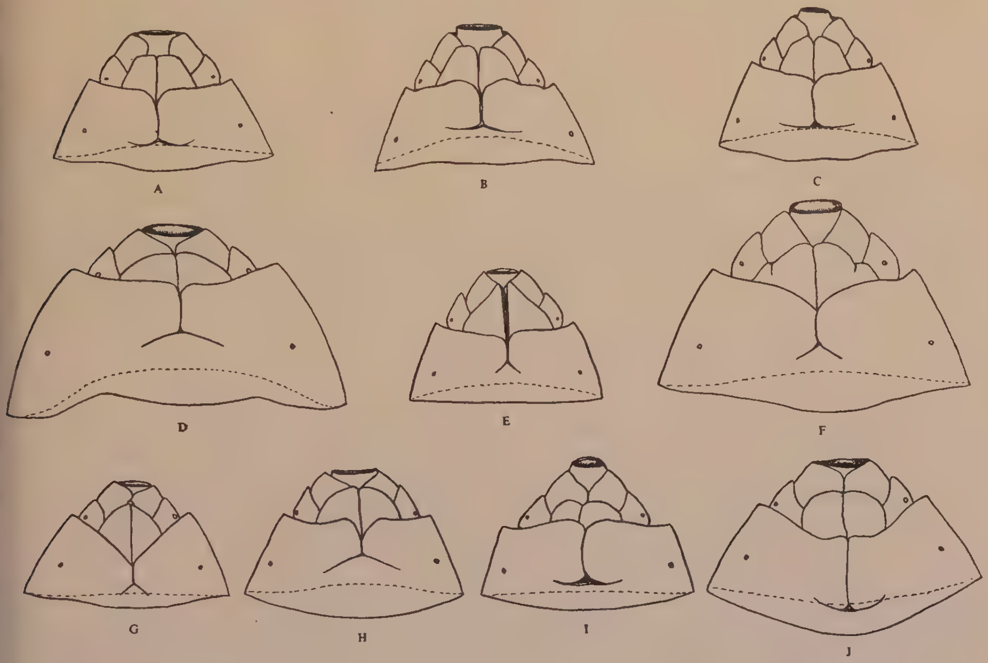


Fig. 11.—Underside of tip of female abdomen. (A) *Pseudotheraptus wayi*, sp. n.; (B) *Ps. devastans* (Dist.); (C) *Ps. ugandae*, sp. n.; (D) *Galaesus hasticornis* (Thnb.); (E) *Theraptus carmelita* (Burm.); (F) *Dasynus coccocinctus* (Burm.); (G) *Dasynus nigromarginatus* (Dist.); (H) *Amblypelta cocophaga* China; (I) *A. bilineata* Stål; (J) *Plinachtus pungens* Thnb. For labelling of parts and segments, see fig. 4. The approximate position of the posterior margin of the 6th segment is indicated by a dotted line. (× 8).

Kenya: Shimba Hills, 1,000 ft., vii.1939 (5 specimens from the Coryndon Museum, lent through the kindness of Mr. E. Pinhey).

Zanzibar: on *Anacardium occidentale* and *Citrus*, 20.x.1953 (*F. L. Vanderplank*).

This distribution is certainly curious for a single species, and it is possible that with more material a separation into subspecies would become necessary.

Theraptus maculatus Schout. is the only species described which is congeneric with *Th. carmelita*. The male pygophore is of similar general form, as is the head, and the two species may be separated by the following key:—

Pygophore of male narrower in rear view, with median lobe more pointed and lateral lobes smaller and more rounded (fig. 6, E). Pronotal collar more pronounced. Antennae mainly black, 1st segment longer than 2nd. Hemelytra unicolorous, pale fawn. Ocelli pink. Sterna with transversely elongated lateral black markings at the bases of the segments (fig. 8, A & B) .... *carmelita* Stål

Pygophore broader in rear view, with median lobe rounded and lateral lobes larger (fig. 6, F.). Pronotal collar less pronounced. Antennae dark brown, 2nd segment longer than 1st. Hemelytra with outer margin darkened. Ocelli colourless. Sterna with longitudinally elongated median and lateral black markings, in addition to basal transversely elongated markings, the latter less conspicuous (fig. 8, C & D) .... *maculatus* Schout.*

Dasynus Burmeister 1834.

This is a large heterogeneous assemblage of species which could with advantage be subdivided, but this would require further study. However, if we take the type species, *D. coccocinctus* Burm., as typical, *Pseudotheraptus* may be separated from it by the absence of a pronotal collar, the presence of shining, raised black spots on the thoracic pleura and the thickened 1st antennal segment (fig. 12, A–C & G); also by the male pygophore, which in *Dasynus* has the posterior margin entire (*i.e.*, not emarginate in the centre) and lacks the characteristic lateral processes of *Pseudotheraptus*, and is divided by a well-marked transverse septum (fig. 6, H; fig. 9, D; fig. 10, E); the transverse fold in the female 7th abdominal sternum is angulate in the centre in *Dasynus*, and cell *m-cu* of the hemelytra is strongly divergent posteriorly (fig. 13, H); the posterior lobe of the peritreme of the scent gland is shorter in *Dasynus*, and the length of the scutellum is greater than the width (41:35 in males, 29:24 in females).

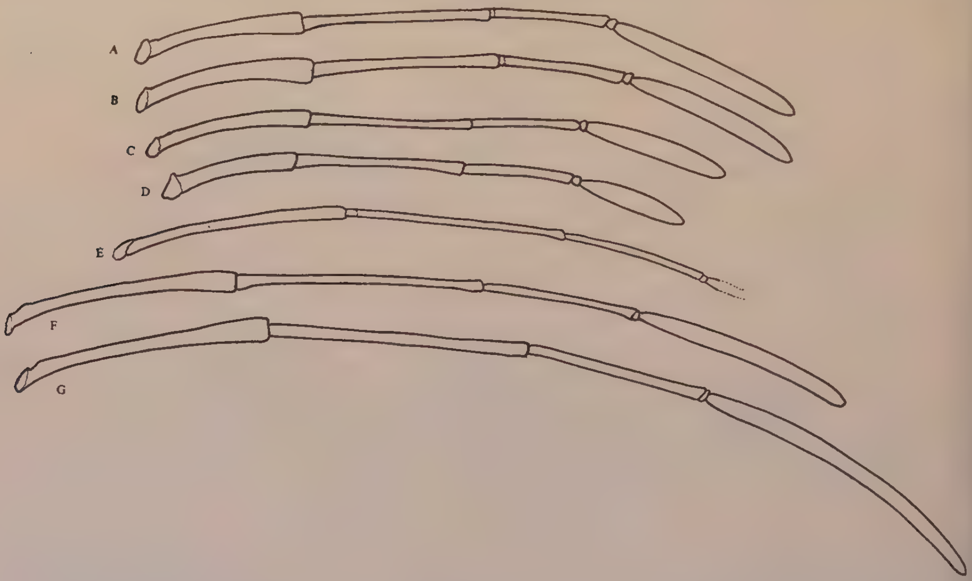


Fig. 12.—Right antennae of males, dorsal view. (A) *Pseudotheraptus devastans* (Dist.); (B) *Ps. wayi*, sp. n.; (C) *Ps. ugandae*, sp. n.; (D) *Plinachtus spinosus* Stål; (E) *Theraptus carmelita* (Burm.) (4th segment missing); (F) *Amblypelta cocophaga* China; (G) *Dasynus coccocinctus* (Burm.). (× 8).

---

* It should be mentioned that the female specimen recorded by Schouteden (*loc. cit.*) as doubtfully conspecific with the male holotype, is here accepted as being conspecific; both specimens have been examined.

Galaesus Dallas 1852 (= *Pendulinus* Thunberg 1822).

This genus differs from *Pseudotheraptus* in the following features: the pronotal disc is more raised, the humeral angles are rounded and not prominent, and the lateral margins often convex; cell *m-cu* is strongly divergent posteriorly (fig. 13, G); the 1st antennal segment is not inflated apically, the 2nd and 3rd are subequal (the 3rd strongly dilated in the genotype *G. hasticornis* (Thnb.)); the mesosternum has no trace of a median longitudinal groove; the posterior margin of the male pygophore is characteristic, with a rectangular median lobe and small indentations on each side of it, and the cavity is divided by a transverse septum (fig. 10, D); the parameres are characteristically shaped, thickened at the base and curved apically (fig. 14, H).

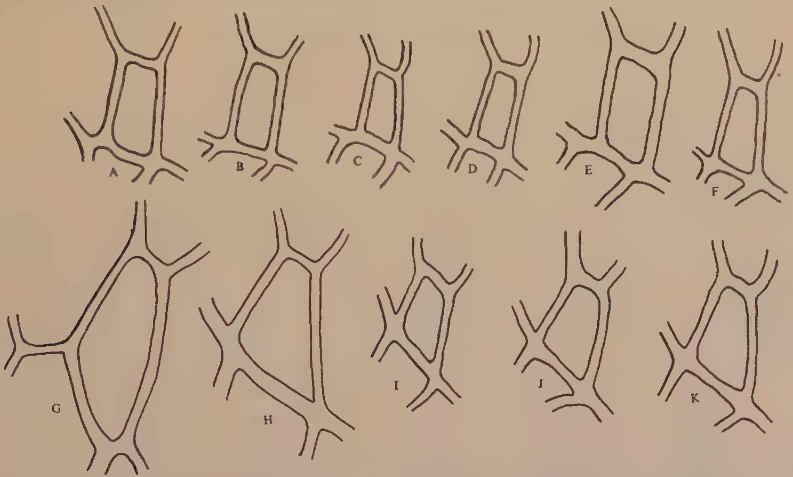


Fig. 13.—Cell *m-cu* of right elytron. (A) *Pseudotheraptus wayi*, sp. n.; (B) *Ps. devastans* (Dist.); (C) *Ps. ugandae*, sp. n.; (D) *Plinachtus spinosus* Stål; (E) *Pl. pungens* (Thnb.); (F) *Theraptus carmelita* (Burm.); (G) *Galaesus hasticornis* (Thnb.); (H) *Dasynus coccocinctus* (Burm.); (I) *D. bucculentus* Stål; (J) *Amblypelta cocophaga* China; (K) *A. gallegonis* Lever. (× 8). (N.B. Allowance should be made for considerable individual variation in using these figures.)

Amblypelta Stål 1873.

The relationship of *Pseudotheraptus* to this genus is of particular interest because *Pseudotheraptus wayi* in East Africa and *Amblypelta cocophaga* China in the British Solomon Islands both feed on developing coconut fruits and produce closely similar if not identical effects known as gummosis or early nutfall (Way, 1951, 1953; Phillips, 1940).

In studying this relationship, it should be mentioned that the type species of *Amblypelta* (*A. bilineata* Stål) differs considerably in both male and female genitalia from the species which have since been added to the genus; the pygophore in the holotype (the only male available to the author) is damaged, but appears to have a median process on the posterior margin with a groove on either side, in which lie the unusually long, protruding parameres. In the other species I have seen, including *A. cocophaga*, the posterior margin is entire and the parameres are short and included entirely within the cavity of the pygophore (fig. 6, I; fig. 9, E; fig. 14, G). In the 7th abdominal segment of the *A. bilineata* female (based on a female from Lifu Is. which appears to be conspecific with or extremely closely allied to the male type from New Caledonia) the ventral fold is strongly sinuate and scarcely angulate in the middle (fig. 11, I), which is the condition found in Gonocerini; while in *A. cocophaga* and other species (fig. 11, H) the fold is straight-sided and angulate centrally as in most other Dasynini. All the species, however, have the truncate, infuscate tip to the scutellum which distinguishes the genus.

The relationship between *A. bilineata* and other species of the genus must await further study when more material is available, but in the meantime the following comparison is based on *A. cocophaga* and other similar species; *Amblypelta* in this sense differs from *Pseudotheraptus* in the following characters:—

(1) The tip of the scutellum is truncate and infuscate.
(2) There are no raised black spots on the thoracic pleura.
(3) Cell *m-cu* of the hemelytra is divergent posteriorly (fig. 13, J & K).
(4) The posterior lobe of the peritreme of the scent gland is short as in *Dasynus*.
(5) The antennae are longer, especially the 3rd and 4th segments, the latter being by far the longest; the 1st segment is not inflated apically (fig. 12, F).
(6) The pygophore of the male has the posterior margin entire in the centre, lacks the tongue-like lateral processes of *Pseudotheraptus* and has a transverse septum, well developed and visible from the rear (fig. 6, I; fig. 9, E).
(7) The parameres have a right-angled bend in the middle (fig. 14, G).
(8) The transverse fold in the 7th sternum of the female is angulate in the centre (fig. 11, J).

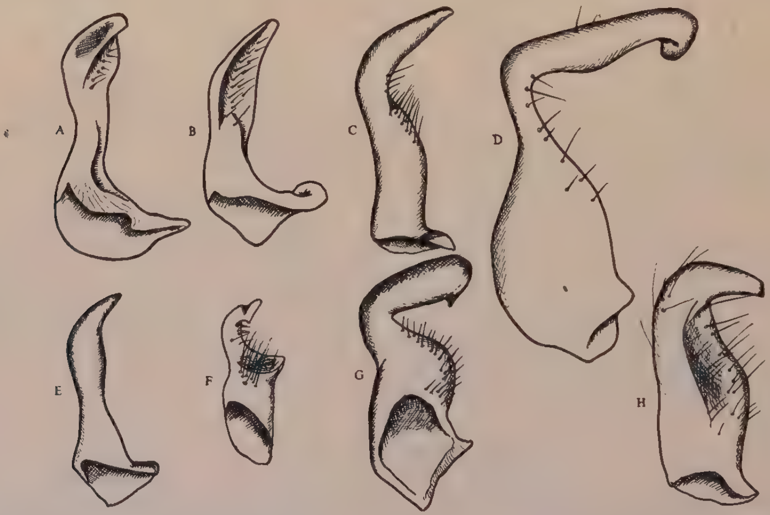


Fig. 14.—Left paramere of male, inner view. (A) *Pseudotheraptus wayi*, sp. n.; (B) *Ps. devastans* (Dist.); (C) *Plinachtus spinosus* Stål; (D) *Dasynus coccocinctus* (Burm.); (E) *Theraptus carmelita* (Burm.); (F) *Dasynus nigromarginatus* (Dist.); (G) *Amblypelta cocophaga* China; (H) *Galaesus hasticornis* (Thnb.). (× 46).

It may be judged from this that although there is a superficial resemblance between the two genera in size and general appearance, there are more fundamental distinctions between them at least as great as those between *Pseudotheraptus* and any other genus of the Dasynini.

Other genera described in the tribe Dasynini are not important for our present purpose. They are as follows: *Odontoparia* Mayr, which is doubtfully distinct from *Dasynus* (see Stål, 1873); *Anadasynus* China and *Paradasynus* China (see China, 1934); *Pseudopendulinus* Schout. (see Schouteden, 1938). *Aulacosternum* Dall. is very distinct (see Stål, 1873), as are also *Jalina* Dist. and *Piramurana* Dist., which have sometimes been placed in this group (see Distant, 1911); they should probably be removed from the Dasynini.

Tribe GONOCERINI Schouteden 1938.

(= Div. *Gonoceraria* Stål, 1873, etc.).

There is also agreement in a number of striking characters between *Pseudotheraptus* and the tribe Gonocerini, and particularly the genus *Plinachtus* Stål, 1859, to which the following remarks apply. These characters are as follows:—

(1) The thickened 1st antennal segment (fig. 12, D).
(2) The absence of a pronotal collar (present in several Dasynine genera) (fig. 1, D).
(3) The presence of raised, shining black spots on the thoracic pleura.
(4) The parallel-sided cell *m-cu* of the hemelytra (fig. 13, D & E).
(5) The median emargination in the hind border, and the absence of a transverse septum in the cavity of the pygophore of the male (fig. 6, D; fig. 7, E; fig. 10, B).
(6) The complex arrangement of conjunctival appendages on the penis (fig. 16).
(7) The long median cleft in the 7th abdominal segment of the female, extending usually beyond the middle of the segment (fig. 11, J).
(8) The tendency to sinuosity in the ventral fold of the same segment of the female, and to the concealment of this fold by the overlapping 6th sternum. In this character, as stated above, *Pseudotheraptus* is, however, intermediate between *Plinachtus* and most Dasynine genera.

There are, by contrast, other characters which *Pseudotheraptus* shares with most Dasynine genera and separate it from *Plinachtus*:—

(1) The 4th antennal segment is long, usually considerably longer than the 3rd and sometimes longer than the 1st and 2nd. The relative lengths of antennal segments is, however, subject to much intrageneric variation (*e.g.*, in *Theraptus*).
(2) The rostrum is longer (with the 4th segment longest), often reaching or

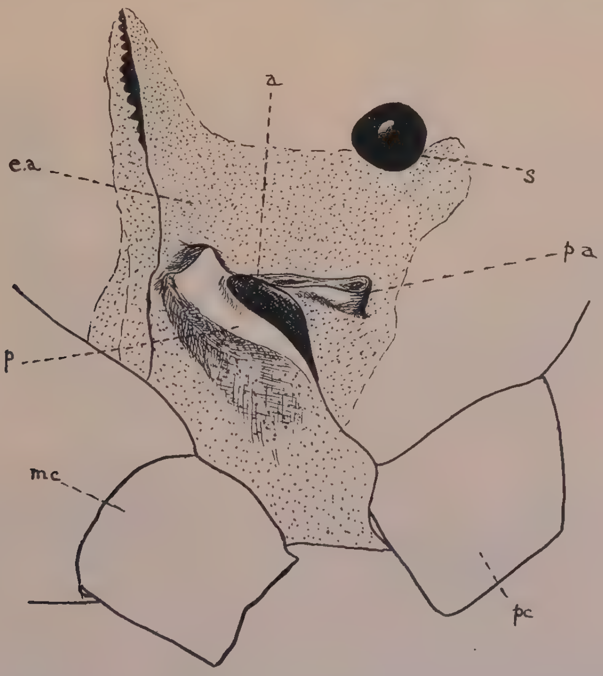


Fig. 15.—Lower part of left metapleuron of *Pseudotheraptus wayi*, sp. n., showing scent gland and raised black spot (*s*). *a*, aperture of scent gland; *e.a*, evaporating area; *mc*, middle coxa; *p*, peritreme; *p.a*, posterior arm of peritreme; *pc*, posterior coxa. (× 36).

surpassing the posterior acetabula. This also is not a consistent generic or group character, for some Dasynine species have the rostrum as a whole, and the 4th segment, shorter.

(3) The puncturation of the pronotum is more even; in *Plinachtus* the distribution of punctures is irregular.

There are other characters again which separate *Pseudotheraptus* from *Plinachtus*, but without necessarily showing general Dasynine affinities:—

(1) The 1st antennal segment is terete, while in *Plinachtus* it is flattened beneath.

(2) It lacks the distinct transverse impression behind the anterior callus of the pronotum, present in *Plinachtus* (fig. 1, D).

(3) The humeral angles of the pronotum are unarmed; in *Plinachtus* they have long, forwardly directed spines (fig. 1, D).

(4) *Plinachtus* lacks the long tongue-like anterior prolongations of the lateral processes of the male pygophore; the processes are short, angular and slightly rolled inwards (fig. 10, B & C).

(5) The ventral fold of the 7th abdominal sternum of the female is less sinuate, and usually with an appreciable, although weakly developed angular median projection (fig. 11, A–C & J).

(6) The penis of *Pseudotheraptus* lacks the median conjunctival appendage found in addition to the lateral pairs in *Plinachtus* (fig. 16).

(7) The spiracles of the 7th abdominal segment of the female are nearer to the

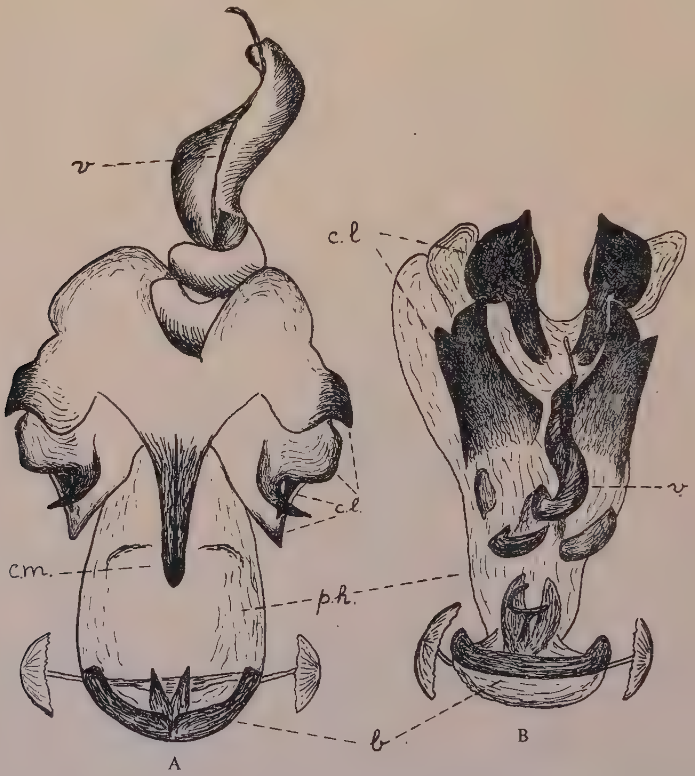


Fig. 16.—(A) Aedeagus of *Plinachtus pugionatus* Stål, in everted condition. (B) Aedeagus of *Pseudotheraptus wayi*, sp. n., partly dissected but not everted. *b*, basal plate; *c.l*, lateral conjunctival appendages; *c.m*, median conjunctival appendage; *p.h.*, phallosoma (= theca); *v*, vesica, surrounded by spiral endosomatic support. (Highly magnified.) (Acknowledgements to Dr. W. E. China, who made the drawing for A.)

front than the hind margin of the segment (they are more or less equidistant in *Plinachtus*).

It will be appreciated from this analysis that there is at least as much justification for placing *Pseudotheraptus* in the Gonocerini, close to *Plinachtus*, as in the Dasynini. *Ps. ugandae* especially, with its shorter 4th antennal segment, pronounced humeral angles and in the form of the male pygophore (compare C & D in fig. 6), comes very close to *Plinachtus*. Clearly the two tribes are imperfectly separable, and there is some justification for uniting them; but before taking this course it will be necessary to study further all the genera involved.

General Conclusions.

A point of general interest from an economic angle is the striking similarity in the coconut-feeding habit, found in the newly described *Pseudotheraptus wayi* on the one hand, and in *Amblypelta cocophaga* on the other. On account of this the view has sometimes been expressed that these two species might really be congeneric, and that one might have evolved from the other; in this event the connection with coconuts need have arisen only once in evolution.

The available evidence, however, clearly indicates the contrary, and may be summarised as follows:—

Taxonomic.—It has been pointed out that while *Amblypelta* is a typical Dasynine genus, *Pseudotheraptus* has affinities also with the Gonocerini. The diagnostic features of the two genera are clearly circumscribed; and furthermore they differ from one another quite as strongly as *Pseudotheraptus* does from other Dasynine genera, and if anything more so than it does from the Gonocerine genus *Plinachtus*.

Geographical.—The three species of *Pseudotheraptus* are all from tropical Africa, while all the known species of *Amblypelta* are confined to the East Indies, North Australia and the South-West Pacific. A wide gap thus separates the areas of distribution of the two genera, which have almost certainly evolved independently, in geographical isolation.

Feeding habits.—Within each of the two genera, connection with coconuts is known only in one species. In *Pseudotheraptus*, the recorded distribution of *Ps. ugandae* is entirely, and of *Ps. devastans* partly, outside coconut-growing regions; the latter species has been recorded feeding on *Manihot utilissima*. In *Amblypelta*, one species (*A. lutescens* (Dist.)) is a pest of bananas, and also of the Macadamia nut (*Macadamia ternifolia*).

Nothing else appears to be known of feeding habits in other species of either genus, but it seems unlikely that there is any question of a common ancestral coconut-feeding habit.

One can assume therefore with some confidence that this habit has arisen independently in one species only of each genus; in neither species is the habit obligatory, since both are known to feed also on other plants.

Summary.

A new genus, *Pseudotheraptus*, is described for a Coreid bug, *Ps. wayi*, sp. n., causing early nutfall of coconuts in East Africa. Two other species, *Ps. devastans* (Dist.) and *Ps. ugandae*, sp. n., are placed in this genus, with descriptions and a key for determination of the three species.

The taxonomic relation of *Pseudotheraptus* to other genera is discussed, with particular reference to *Theraptus*, in which the species now described as *Ps. wayi* was formerly placed provisionally, and to *Amblypelta*, of which one species (*A. cocophaga* China) is the cause of identical damage to coconuts in the British Solomon Islands Protectorate.

A key is given for the determination of the two species now remaining in the genus *Theraptus*.

Acknowledgements.

I wish to express my thanks to Dr. W. J. Hall, C.M.G., Director of the Commonwealth Institute of Entomology, for suggesting and giving facilities for this investigation; to Mr. E. O. Pearson, Assistant Director of the same Institute, for assistance in obtaining material for study; and to Dr. W. E. China, British Museum (Nat. Hist.), for much help and suggestions in connection with the taxonomic work, and for making the drawing for part of fig. 16. Finally, I wish to thank the following, who have helped with information or by kindly sending specimens for study: Dr. R. H. Le Pelley, Dr. F. L. Vanderplank, Mr. W. J. Way, Mr. G. Swaine, Mr. E. Pinhey (Coryndon Museum, Nairobi), Mr. P. Basilewsky (The Congo Museum, Tervuren), Dr. R. Malaise (Naturhistoriska Riksmuseum, Stockholm), and Prof. G. C. Varley (The Hope Department, Oxford).

References.

Bergroth, E. (1913). Supplementum catalogi Heteropterorum Bruxellensis. II. Coreidae, Pyrrhocoridae, Colobathristidae, Neididae.—Mem. Soc. ent. Belg., **22,** pp. 125–183.

Blöte, H. C. (1935). Catalogue of the Coreidae in the Rijksmuseum van natuurlijke Historie. Part II. Coreinae, first part.—Zool. Meded., **18,** pp. 181–227.

Burmeister, H. (1834). Rhyngota seu Hemiptera . . .—Nova Acta Leop. Carol., **16,** suppl. 1, pp. 285–306.

China, W. E. (1934). A new species of Coreidae (Heteroptera) injurious to coconut in the Solomon Islands.—Bull. ent. Res., **25,** pp. 187–189.

Dallas, W. S. (1852). List of the specimens of Hemipterous insects in the collection of the British Museum. Part II, pp. 440–441. London.

Distant, W. L. (1911). Rhynchotal notes. LV. Australasian Coreidae and Berytidae.—Ann. Mag. nat. Hist., (8) **7,** pp. 576–586.

Distant, W. L. (1917). Some insects injurious to cacao plants in the Belgian Congo. Order Rhynchota.—Bull. ent. Res., **8,** p. 118.

Lethierry, L. & Severin, G. (1894). Catalogue général des Hémiptères. Tome II.—277 pp. Brussels, Mus. Hist. nat. Belg.

Phillips, J. S. (1940). Immature nutfall of coconuts in the Solomon Islands.—Bull. ent. Res., **31,** pp. 295–316.

Schouteden, H. (1938). Catalogues raisonnés de la faune entomologique du Congo Belge. Hémiptères, Coreidae.—Ann. Mus. Congo belge, Zool. (3) Sect. ii, **1,** pp. 221–308.

Snodgrass, R. E. (1933). Morphology of the insect abdomen. Part II.—Smithson. misc. Coll., **89,** no. 8, 148 pp.

Stål, C. (1859). Till kännedomen om Coreida.—Öfvers. VetenskAkad. Förh., **16,** pp. 449–475.

Stål, C. (1873). Enumeratio Hemipterorum.—Kl. svenska VetenskAkad. Handl., **11,** no. 2, 163 pp.

Tait, E. M. (1954). Some experiments in cross-breeding of the Coreid bug, *Theraptus* sp.—Bull. ent. Res., **45,** pp. 433–435.

Thunberg, C. P. (1822). Dissertatio entomologica de Hemipteris rostratis capensibus, **4,** p. 5.

Way, M. J. (1951). An insect pest on coconuts and its relationship to certain ant species.—Nature, Lond., **168,** p. 302.

Way, M. J. (1953). Studies on *Theraptus* sp. (Coreidae); the cause of the gumming disease of coconuts in East Africa.—Bull. ent. Res., **44,** pp. 657–667.

VARIATION IN THE HATCHING-RESPONSE OF *AËDES* EGGS (DIPTERA: CULICIDAE).

By J. D. Gillett

East African Virus Research Institute, Entebbe, Uganda.

In the genus *Aëdes* Meigen, eggs laid by a single female in one batch and kept submerged in a single container may hatch in instalments over a very long period. Furthermore, on one occasion a high proportion of the eggs may hatch within a given time, while on another, under similar conditions, very few may hatch. The advantage of scattered hatching to a species which tends to lay its eggs in small collections of water subject to irregular fluctuations in level is evident; if the water dries and the larvae or pupae from the first hatch are lost, there will be more eggs to benefit from subsequent and perhaps more prolonged flooding. The present work was undertaken to investigate this erratic hatching-response and to test all the obvious variables, other than genetic ones, that might contribute to it.

It has long been recognised that certain changes in the environment may act as hatching-stimuli to the eggs of *Aëdes*. Although it is clear that some stimuli are more effective than others, the extremely erratic hatching-behaviour of the eggs makes it difficult to assess accurately the relative merits of various stimuli, and these will not be dealt with here, except in so far as they bear on the problem.

Terminology.

Before describing the investigation of the hatching-response of *Aëdes* eggs, it is necessary to define some of the terms as they will be used here.

Maturity. An egg that has completed its embryonic development and is anatomically *mature* is regarded as being potentially capable of hatching, whether it does so or not; correspondingly, an anatomically *immature* egg is taken to be incapable of hatching.

Diapause. An *Aëdes* egg does not necessarily hatch as soon as it becomes mature, even though conditions are known to be compatible with hatching, as judged by the fact that companion eggs are hatching in the same container. This usual but highly variable delay between an egg becoming mature and hatching will be considered here as an example of *diapause*.

Past work has indicated that various hatching-stimuli differ in their effectiveness. Strong stimuli will induce hatching in a high proportion of mature eggs, weak stimuli will induce hatching in a low proportion. It seems reasonable to assume that an egg that responds to a weak stimulus would necessarily respond to all stronger stimuli. If this is true, then the strength of the stimulus required to produce hatching must vary from egg to egg. In other words, the *depth* of diapause must vary from egg to egg. Now it is clearly impossible ever to exclude chance, uncontrolled changes in environment as the cause of hatching in those eggs that hatch in the absence of deliberate stimulation, and so it will be taken as axiomatic that hatching always requires some stimulus. The corollary to this, which will also be accepted throughout this study, is that all eggs are to some extent in diapause up to the moment they hatch. In these terms, the depth of diapause of any egg may be considered as varying with the passage of time, and the manner of this variation with time must itself vary from one egg to another. The following work will be treated as a study of the distribution and changes with time of the depth of diapause in *Aëdes* eggs.

Batch variation. The eggs laid by a single female *Aëdes* following a blood-meal will be taken to constitute a *batch* of eggs. Differences in the hatching time of the eggs in a single batch, kept under identical conditions, can be termed *intra-batch variation*, and differences in the hatching time of the eggs in different batches, *inter-batch variation.*

Pregnancy. The interval between the taking of a blood-meal and the laying of a batch of eggs by a mated female is, for convenience, referred to as *pregnancy.*

General Methods.

The experiments to be described were carried out in the East African Virus Research Institute, Entebbe, Uganda, which is situated about 3,900 feet (1,188 metres) above sea-level. The temperature in the laboratory remains fairly constant at 22–26°C. throughout the year, but sometimes drops to 20°C. or below for short periods, especially during thunderstorms.

Except where otherwise stated, *A.* (*Stegomyia*) *africanus* (Theo.) and *A.* (*S.*) *aegypti* (L.) were used in these experiments. Adults of the former species were caught at Lunyo, near Entebbe; adults of the latter species were reared from pupae that had been removed from the Institute mosquito colony*. The mosquitos were isolated individually in small sterilised glass tubes, 25 × 80 mm. The method of keeping them is a modification of that used by Bates & Roca-Garcia (1945) and has been fully described by Ross & Gillett (1950). The caught female *A. africanus* were presumed to have mated before capture and this was confirmed by the observation that, with one exception, all batches of eggs laid by them were later shown to be fertile. On the other hand, the reared *A. aegypti* had to be mated in captivity. Each mosquito was fed on blood from the writer and maintained on raisin during pregnancy. Preliminary observation showed that large quantities of brown-coloured excreta were passed on the third day after the blood-meal. On the evening of the third or the morning of the fourth day, therefore, when no further visible contamination of the tubes took place, the insects were transferred individually to the laying-tubes, which were small sterilised glass tubes, 14 × 85 mm., containing a strip of Balston's No. 1 filter paper arranged as shown in fig. 1. This arrangement kept the surface of the paper uniformly moist. The tubes were inclined at about 5° to the horizontal and the open ends were plugged with cotton-wool as shown in fig. 1. Sterile distilled water was used in the tubes.

The laying-tubes were examined morning and evening, so that a batch of eggs found at the morning examination would be less than 16 hours old and at the

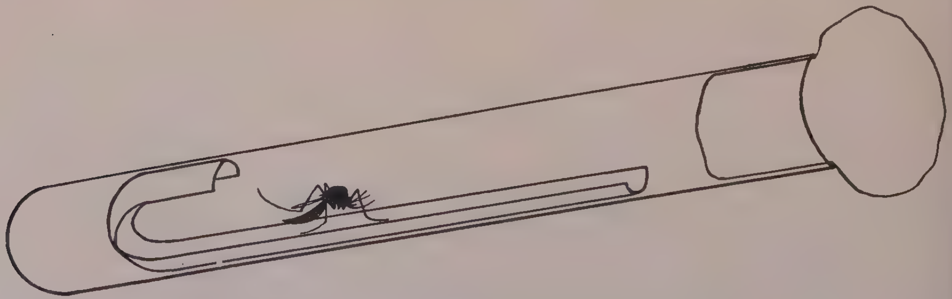


Fig. 1.—Laying-tube, showing arrangement of filter paper in the tube. The paper is kept moist by being in contact with distilled water at the bottom of the tube.

---

* This colony was started in 1947 from eggs sent from Lagos, Nigeria, by Dr. J. C. Bugher.

evening one, less than eight hours old. On discovery of a batch of eggs, the filter paper bearing them was transferred to a vertical tube containing tap-water and put up in an experiment. In all the experiments to be described the day of discovery of the eggs is called Day 0 and, except where otherwise stated, only "morning eggs" were used. Eggs laid on the glass or on the very edge of the filter paper were discarded.

Under these conditions the female mosquito usually lays a batch of 20–100 eggs on the fourth or fifth day after the blood-meal. Each egg is laid separately but remains attached to the moist filter paper on which it is laid, even after the paper has been submerged in water. The eggs when laid are white and do not begin to darken until about an hour after laying. Darkening is complete after another 30 minutes in *A. africanus*, the process being somewhat quicker in *A. aegypti*. At room temperature at Entebbe, development of the embryos takes 5½ to 6½ days in *A. africanus* and 3 to 4 days in *A. aegypti*. This has been shown by the daily opening of eggs and by long series of observations in which the eggs were kept in water containing a small amount of brain-heart infusion and brewers' yeast (Heal & Pergrin, 1945). This medium, hereinafter referred to as BHY, stimulates most of the viable eggs of *A. africanus* and all those of *A. aegypti* to hatch, no matter when it is applied after completion of embryonic development.

Experimental.

This investigation was prompted by the anomalous results obtained when trying to rear large numbers of *A. africanus* for yellow-fever transmission experiments, and the first experiment to be described was originally designed to determine if there was any relation between hatching time and the interval between laying and submergence. It is included here because the unexpected result led directly to a method of daily stimulation, which was used consistently throughout this work. Eighty batches of eggs of *A. africanus*, totalling 3,212 eggs, were submerged at varying intervals from Day 0 to Day 7 and as they became available. Thus one or more batches were submerged on almost every day for a period of over six weeks. Hatching occurred in at least one batch on almost every day from Day 5 to Day 80, but bore no relation to the time of submergence. On one particular day, however, 1,348 (51%) of the remaining 2,650 unhatched eggs hatched. Hatching occurred in 67 out of the 80 batches on this day, when the ages of the eggs still at risk varied from 29 to 75 days. Clearly, any variation in the hatching-response of the eggs of different batches submerged at different times after laying was not enough to mask some uncontrolled variable in the environment, which seemed most likely to be an unexpectedly rapid drop in temperature, of about 5°C., which occurred on that day. Bacot (1916) and Fielding (1919) recorded that a rapid fall in temperature of a few degrees results in the hatching of eggs of *A. aegypti*. This point clearly needed further investigation; if a fall in temperature was found to act as a stimulus to hatching in *A. africanus*, then some or all of the variation in hatching-behaviour may have been due to fluctuations in temperature.

The effect of treatment with cold.

A batch of 35 eggs was submerged on Day 4 and kept at room temperature. On Day 24 the tube of water containing the eggs was placed in a small glass jar of water, which in turn was placed in a tank of water at 9°C. A similar tube of water to that containing the eggs was also submerged in the inner container of the double water-bath and the temperature of the water in it was recorded at intervals. The eggs were viewed continuously under a dissecting microscope. At the beginning of the experiment (Minute 0) the temperature in the tube was 22·4°C. Hatching started at Minute 3·5 when the temperature had fallen to 18·4°C. and continued until Minute 7·5 when the temperature had dropped to 16·0°C. The temperature dropped further, until it reached 13·8°C. at Minute 15 and was then allowed to rise gradually to its original level by Minute 150. No further hatching occurred. Altogether 10 out of the 35 eggs hatched during the first seven and a half minutes. Other experiments gave similar results: some hatching usually occurred provided the initial fall in temperature was fairly rapid, but no hatching occurred when the temperature was rising, even when the fall in temperature had been gradual and the subsequent rise sudden. It was concluded that a sudden fall in temperature is adequate as a stimulus to hatching and must almost certainly have accounted for the very large hatch which occurred in nearly all batches on the particular day in question.

This example of a definite uncontrolled environmental factor, causing eggs to hatch irrespective of their age or upbringing, may be exceptional. Haslam (1927) examined the results obtained by Buxton & Hopkins (1927) with *A.* (*S.*) *scutellaris* (Wlk.), but failed to demonstrate any factor tending to cause the eggs in different containers to hatch on particular days. It is clear, however, that experiments with eggs of *A. africanus* demand rigorous control of temperature, particularly, perhaps, at a place such as Entebbe, where sudden falls in temperature occasionally occur in prolonged periods of otherwise steady temperature.

As no constant-temperature room was available, some method had to be

TABLE I.

The overall hatching-response of 20 batches of eggs of *A. africanus* subjected to daily cold treatment for 30 days from the time of laying.

Day	No. eggs at risk	No. eggs hatching		% hatch of eggs at risk
		Before treatment	After treatment	
0	1059	—	—	—
1	1059	0	0	0
2	1059	0	0	0
3	1059	0	0	0
4	1059	0	0	0
5	1059	0	12	1
6	1047	9	108	11
7	930	15	170	20
8	745	4	173	24
9	568	9	172	32
10	387	0	27	7
11	360	1	28	8
12	331	1	13	4
13	317	0	4	1
14	313	0	3	1
15	310	1	64	21
16	245	0	3	1
17	242	0	1	0
18	241	1	7	3
19	233	0	10	4
20	223	1	5	3
21	217	0	0	0
22	217	0	1	0
23	216	0	0	0
24	216	0	1	0
25	215	1	3	2
26	211	0	0	0
27	211	0	1	0
28	210	1	0	0
29	209	0	2	1
30	207	0	1	0

devised for nullifying uncontrolled fluctuations in temperature. A further series of experiments was, therefore, undertaken in an attempt to produce similar conditions in all submerged batches on all days, by lowering the temperature by the same amount and at the same rate in all tubes simultaneously every day. The aim was to give all eggs a daily stimulus greater than that resulting from daily fluctuations in the air temperature.

Variation of hatching-response in the face of daily cold treatment.

Twenty batches of eggs of *A. africanus* were each submerged on Day 0 in 7 ml. tap-water in sterile tubes. Each morning the tubes were examined and, after removal of any hatched larvae, were placed in a refrigerator for 22 minutes. Previous trials with tubes containing the same amount of water had shown that during this period the temperature dropped to between 15 and 13°C., depending on the initial temperature in the room. This treatment was given daily from Day 1 onwards. The overall hatching-response of the twenty batches up to Day 30 is shown in Table I.

Although most of the hatching occurred soon after maturity, hatching of eggs is seen to be scattered over the whole period from Day 5 to Day 30. (Half of the batches were in fact treated daily until Day 150, and amongst these hatching occurred as late as Day 124.) The behaviour of individual batches indicated that this variation in the hatching time of eggs occurs both between batches and within batches. The results for four selected batches will suffice to show the extreme diversity of response in different batches (Table II).

TABLE II.

The hatching-response of four batches of eggs of *A. africanus* subjected to daily cold treatment from the time of laying.

Batch No.	722		728		730		775	
No. of eggs	18		42		83		119	
Day	No. hatched		No. hatched		No. hatched		No. hatched	
	Before cold	After cold	Before cold	After cold	Before cold	After cold	Before cold	After cold
4	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—
6	—	—	—	9	—	1	—	12
7	4	12	—	12	—	5	—	2
8	—	—	—	3	—	5	—	1
9	—	—	—	6	2	70	—	2
10	—	—	—	—			—	4
11	—	—	—	1			—	17
12	—	—	—	1			—	5
13	—	—	—	—			—	—
14	—	—	—	—			—	—
15	—	—	—	—			1	56
19	—	—	—	1			—	—
32	—	—	—	1			Discontinued after Day 30	
42	—	—	1	—				
43	—	—	2	—				
44	—	—	—	2				
58	—	—	—	1				
124	—	1	—	—				
Percentage hatched by Day 9	89		71		100		14	

Batch 775 is of particular interest; it will be seen that scattered hatching following cold treatment occurred from Day 6 to Day 12. On Day 15, however, one egg hatched prior to cold treatment and this was followed by a further 56 after cold treatment. It would seem that the depth of diapause in this one egg had decreased to what may be called the threshold of spontaneous hatching (*i.e.*, hatching without deliberate stimulation) and that more than half of the remaining unhatched eggs in the batch, although not reaching this level, had simultaneously passed the level at which response occurs to cold treatment. If this is so then half of the eggs in this batch must have been extraordinarily alike. The phenomenon of isolated "spontaneous" hatching before cold treatment being followed by a large hatch after cold treatment on the same day was by no means uncommon and occurred as late as Day 73. Young (1922) found that the presence of a single larva would bring about hatching of eggs of *A. aegypti* present in the same container. It is possible that in these cases with *A. africanus*, the presence of the single spontaneously hatched larva provides a subliminal stimulus for the other eggs, which, by summation, results in a lowering of the threshold of response to cold treatment.

Irrespective of possible changes in the depth of diapause and the possibility of summation of subliminal stimuli, it is clear that the hatching of eggs of *A. africanus* is controlled by a property which is quantitatively variable and is distributed unevenly, not only between batches but also within them. The existence of intra-batch variation of response means that certain factors may at once be excluded as a single basis for that variation. Thus, the age of the female at the time of laying cannot conceivably account for variation in the behaviour of the eggs she lays on a single occasion, unless the distribution among her eggs of some unique property is itself a function of her age. Also, differences in the general external environment cannot account for variation in the behaviour of eggs of the same batch kept in a single container. It would seem, therefore, that differences in the eggs themselves must determine their subsequent hatching-behaviour. In other words, some quantitatively variable factor in the egg, or supplied with the egg, must determine not only the depth of diapause in that egg but also the changes of depth with time.

Possible Sources of Variation between Eggs.

Apart from inherited differences, which form the subject of a separate paper (Gillett, 1955), there are a number of factors operating during the sequence of events leading up to the laying of the eggs and, indeed, up to the time that the eggs reach maturity, which could conceivably influence the hatching-response. These possible sources of variation can be classified according to whether they operate before, at or after the moment of laying:—

(i) *Before laying.* While in this genus a single mating followed by a single blood-meal is usually adequate for the production of a batch of fertile eggs, there is no reason to suppose that the number of matings and number of blood-meals is always limited to one. Thus, there may at least be scope for variation between females both in the number of matings before the first blood-meal and in the number of blood-meals during pregnancy.

(ii) *At the time of laying.* About four days after the first blood-meal, the eggs are laid one by one to form a batch, each egg being attached to the substratum, possibly by some substance accompanying it. Thus, eggs vary one from another in the order in which they are laid and they may perhaps vary in the amount of this accompanying substance.

(iii) *After laying.* The eggs in a batch are laid one by one in any position on the nearly horizontal paper over a period of one or more hours. Thus, when the paper bearing the eggs is finally submerged in the vertical tube, the eggs must vary one from another, both in age and in their orientation with respect to gravity.

The differences outlined above are the obvious ones occurring between batches and between eggs laid in a single batch, and they are dealt with in the next section, without speculation on the ways in which they might be supposed to exert their effect on subsequent hatching-behaviour; for convenience, they will be considered in the reverse of the order in which they occur.

(*a*) *The orientation of the egg with respect to gravity.* A batch of 33 eggs of *A. africanus* was submerged on Day 4 and kept in the vertical plane for 20 days, the positions of the eggs having been recorded (fig. 2). On Day 24 the tube containing the eggs was placed in a double water-bath as described previously and the temperature was dropped. The eggs were kept under observation and those that hatched were marked on the figure. At the end of the experiment, the remaining unhatched eggs were opened and found to contain mature embryos. Reference to fig. 2 will show that the orientation of the eggs in relation to gravity played no part in selecting the ten eggs that responded to the change in the external environment.

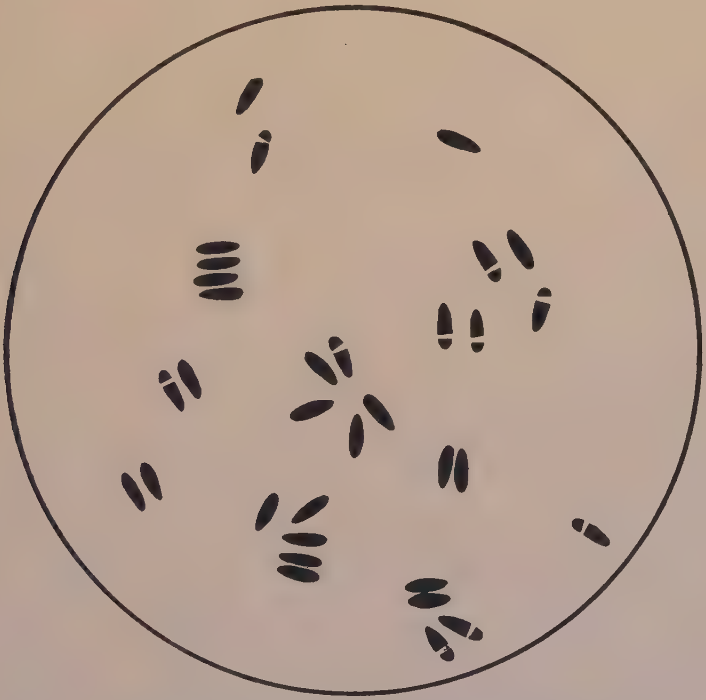


Fig. 2.—Batch of eggs of *A. africanus* after treatment with cold. The hatched eggs are shown with their caps separated.

(*b*) *Small differences in age at the time of submergence.* Female *A. africanus* were kept under observation during oviposition and portions of the resulting egg-batches were submerged at varying intervals from 15 minutes onwards. The results are shown in Table III. These have been presented in full, as combination of the results would be misleading on account of inter-batch differences. There is no evidence that intra-batch variation has any association with small age differences at the time of submergence.

(c) *Fixed and unfixed eggs.* Eggs of *A africanus* can be slid over the moist surface of the filter paper on which they are laid and will continue to adhere to the paper even when it is submerged in water, soap solution, alcohol or ether. If, however, they are rolled over or lifted, or contact with the moist paper is otherwise broken, they will become detached and sink (or float) when the paper is subsequently submerged. Christophers (1945) suggested that in the genus *Culex* L. surface forces may be responsible for cohesion of the eggs, and it is possible that something of this sort may be operating in *A. africanus* and other species of *Aëdes* that lay fixed eggs. It seems possible, however, that the ovipositing female provides a secretion that allows or causes attachment of the eggs to the substratum (that this is not in the nature of a hardening cement is clear from the foregoing) and that the amount of this secretion varies with each egg laid.

TABLE III.

Effect of small age differences at the time of submergence on the hatching-response of eggs of *A. africanus*.

	Daily cold treatment from Day 1 onward						Daily cold treatment from Day 9 onward			
Batch No.	826				827		828		829	
Sub-batch	1	2	3	4	1	2	1	2	1	2
Age in hours when submerged	½	1	2	6	¼	18	½	7	¼	2
No. of eggs	8	3	10	8	18	28	20	13	22	14
Day 5–	—	—	—	—	—	—	—	—	—	—
,, 6–	2	1	3	1	5	4	—	—	—	—
,, 7–	—	—	1	1	12	22†	—	—	—	—
,, 8–	2	—	3	—	1	2	—	—	—	—
,, 9–	—	—	—	—			18	4	15	10
,, 10–	—	—	—	—			1	4	5	3
,, 11–	—	—	—	—			—	—	—	—
,, 12	4*	2*	3*	6*			1*	5*	2*	1*
Proportion hatched by Day 11	0·50	0·33	0·70	0·25	1·00	1·00	0·95	0·62	0·91	0·93

All eggs submerged on Day 0.

* Hatched after treatment with BHY.

The entry for each day represents the number of eggs that hatched after cold treatment, except for that marked thus †, where one egg hatched before cold treatment.

Female *A. africanus* in the act of ovipositing on moist filter paper were watched under the dissecting microscope. As the eggs emerged from the parent, nearly every second one was caught on the flattened tip of a sterile needle and removed to and wiped across the surface of a second piece of moist filter paper. Each batch was thus divided into two portions, one consisting of eggs which had been attached normally at the time of laying, the other consisting of eggs which had been removed to a fresh piece of paper at the time of laying. There is no certainty that those eggs comprising the removed portion were completely lacking in the hypothetical substance, even though they failed to become fixed in their new position, but it may be presumed that they would tend to have less of the substance attached to them than would those left undisturbed. Thus, if the response to the external stimulus depends on the amount of this substance provided with each egg, one would expect to find an altered hatching-response in one portion.

As it was not always possible to catch the mosquito in the act of laying, the numbers in this experiment are unfortunately few. The temperature was dropped daily until Day 12, when the eggs were transferred to BHY medium. The results are shown in Table IV, from which it will be seen that although the hatch in the moved portion of the batches was in each case a little lower than in the undisturbed portion, there is no significant difference between them.

TABLE IV.

The hatching-response of fixed and unfixed eggs of *A. africanus* subjected to daily cold treatment for 11 days from the time of laying.

Batch No.	Fixed eggs	Unfixed eggs	χ^2	P
821	17/25 (0·68)	7/11 (0·64)	0·16	0·69
822	14/29 (0·48)	4/16 (0·25)	2·02	0·16
824	13/15 (0·87)	8/10 (0·80)	0·31	0·58

Numerator = number of eggs hatching by Day 11.
Denominator = total number of eggs in each sub-batch.
In brackets = proportion of eggs hatching by Day 11.

As stated above, there was no certainty that the removed eggs had less of the hypothetical substance. If, however, intra-batch variation is attributable to differences in the amount of this accompanying substance then there should be a difference in the hatching-response between species of *Aëdes* normally laying fixed eggs and those normally laying unfixed eggs. It seemed advisable to make this comparison, between more than one species of *Aëdes* laying fixed eggs and more than one species laying unfixed eggs, and between different species of the same subgenus laying fixed and unfixed eggs. Accordingly experiments were undertaken with 16 batches of fixed eggs of *A. aegypti*, 10 batches of fixed eggs of *A.* (*S.*) *apicoargenteus* (Theo.) (from Lunyo, near Entebbe), and eight batches of fixed eggs of *A.* (*Finlaya*) *longipalpis* (Grünb.) (from Zika Forest, near Entebbe), and with 10 batches of unfixed eggs of *A.* (*F.*) *ingrami* Edw. (from Lunyo), and five batches of unfixed eggs of *A.* (*Banksinella*) *circumluteolus* (Theo.) (from Lunyo).* The eggs were laid on the moist filter paper in the laying-tubes, but on submergence of the pieces of paper the unfixed eggs of *A. ingrami* and *A. circumluteolus* either floated at the surface or sank to the bottom. Only submerged eggs were used.

All the batches were cold-treated daily until Day 30, when the remaining unhatched eggs were hatched by the addition of BHY. All three species normally laying fixed eggs responded to cold treatment.† In *A. aegypti* and *A. apicoargenteus*, hatching started on Day 3 and continued intermittently throughout the period; in *A. longipalpis*, most of the hatching occurred from Day 11 to Day 15 but some occurred intermittently from Day 15 onward (previous trials with this species had already shown that embryonic development takes 11½–12½ days). On the other hand, in neither species normally laying unfixed eggs was there any response to daily cold treatment, notwithstanding the fact that it was shown that the period of embryonic development is not more than 14 days in *A. ingrami* and not more than six days in *A. circumluteolus*. All the eggs of the latter species were hatched on addition of BHY on Day 30 but those of *A. ingrami* needed repeated applications of this stimulus before all the eggs hatched.

---

* The eggs of *A. ingrami* and *A. circumluteolus* resemble those of the European *A.* (*Ochlerotatus*) *rusticus* (Rossi) in their diamond-shaped outline when viewed dorsally. It is possible that failure to become attached to the substratum depends on the shape of the egg. It is interesting to note that the fixed eggs of *A.* (*F.*) *longipalpis* resemble those of the various species of *Stegomyia* used, in their long sausage-shape.

† To these three may be added *A.* (*S.*) *ruwenzori* Haddow & van Som., the eggs of which are of the fixed type and hatch in instalments after successive treatment with cold from Day 16 to Day 44 (Gillett, 1951).

Thus, while no evidence was produced to refute the possibility that response of the eggs to cold treatment is in some way determined by the amount of some substance laid with the eggs by the mother, the evidence favouring it was too indirect to allow any conclusions to be drawn.

(*d*) *The order of laying*. Pregnant females of *A. africanus* were kept under observation on the fourth day following a single blood-meal. When oviposition started, each insect was secured by the wings in the tips of fine forceps and was placed on a strip of moist filter paper, which had previously been divided into equal areas by transverse pencil lines. Each mosquito was watched under a dissecting binocular microscope and as soon as a small number of eggs had been laid in the first division she was moved on to the next and so on until she had finished laying the batch. It was not always possible to obtain equal numbers of eggs in each division, nor was it possible to obtain a complete batch on more than a few occasions. As soon as the eggs had darkened, each division was cut off the strip and submerged in a separate tube of water. The temperature was dropped daily until Day 30. The results (Table V) show that although batches vary one from another, intra-batch variation has no association with the order in which the eggs are laid.

(*e*) *The number of blood-meals*. Ten female *A. africanus* were given the opportunity to take a blood-meal twice a day. In each case feeding was observed under a hand lens and fresh blood was seen to enter the stomach until a state

TABLE V.

Effect of order of laying on the hatching-response in single batches of eggs of *A. africanus* subjected to daily cold treatment for 30 days from the time of laying.

Batch No.	Early-laid	Middle-laid	Late-laid	Total
756	16/27 (0·59)	17/26 (0·65)	16/25 (0·64)	49/78 (0·63)
757	18/18 (1·00)	19/20 (0·95)	29/29 (1·00)	66/67 (0·99)
758	32/34 (0·94)	39/44 (0·89)	26/31 (0·84)	97/109 (0·89)
759	21/29 (0·72)	23/31 (0·74)	24/29 (0·83)	68/89 (0·76)
Total	87/108	98/121	95/114	280/343
%	81	81	83	82

Each batch divided into 3 sub-batches (early-, middle- and late-laid).
Numerator = number of eggs hatching by Day 15.
Denominator = total number of eggs in each sub-batch.
In brackets = proportion of eggs hatching by Day 15.

of distension was reached. Even when already distended with eggs and the remains of the previous blood-meal, the mosquitos took in as much blood as there was room for. (One of them fed 23 times in 14 days.) Three of them, although full of eggs, died without laying any of them; three others, also full of eggs, laid only four, six and seven eggs, respectively. The results of the experiment indicated that repeated feeding during pregnancy did not tend to bring about homogeneity of response in a batch. Wholly refractory batches were laid by females which had fed 23, 11 and 6 times during the single pregnancy, while erratic hatching occurred in batches laid by females which had been fed 17, 11 and 8 times. The experiment was not repeated owing to the difficulty in obtaining eggs under these conditions, but it is concluded that if some factor supplied by the mother has an effect on the hatching-response of the eggs, then the distribution of this factor is not influenced by the number of blood-meals taken during pregnancy.

(*f*) *The number of matings of the mother.* All attempts at inducing *A. africanus* to mate in captivity failed, and it was necessary to use *A. aegypti* for this experiment. It has already been shown in the experiments on fixed and unfixed eggs, that the hatching-response of this species resembles that of *A. africanus*. It differs, however, from *A. africanus* in that embryonic maturity is reached in three to four days and there is a less marked outburst of hatching immediately after reaching maturity.

Each of twenty-four virgin female *A. aegypti* (picked out from the colony as female pupae) was mated with one or more males, the number of matings per female varying from one to 40 but no single male being allowed more than two matings. Following a blood-meal, the mated females each laid one batch of eggs but, with the daily stimulus of cold treatment, only 46 out of 1,077 eggs hatched by Day 30. No association could be found between the number of matings and the subsequent hatching-behaviour: wholly refractory batches were laid by females which had been mated 1, 2, 3, 6, 8, 15, 18, 22 and 40 times, while hatching occurred in batches laid by females which had been mated 2, 3, 4, 10, 20 and 30 times. The numbers which hatched were small, however, and before this possibility could be adequately tested, a stimulus would have to be used that would result in larger hatches and would thus allow a better comparison of variation between batches. As no comparison of response was being made between *A. africanus* and *A. aegypti*, it did not matter what the stimulus was, as long as it was of moderate potency for the species being used. The stimulus resulting from one minute's exposure to air was found to be very suitable and was used in a second experiment which is described below.*

Twenty-nine female *A. aegypti* were each mated to one or more males, the number of matings per female varying from one to 15. After a blood-meal, 29 batches of eggs were obtained and each was submerged in a tube of tap-water on Day 0. The tubes were kept undisturbed at room temperature for the first two days. On the morning of Day 3 the tubes were examined as usual, after which the paper bearing the eggs was removed from the water for exactly one minute. During this period any larvae were removed and counted and then the paper was returned to the tube, which had in the meantime been refilled with fresh tap-water. This procedure was repeated in the evening so that every batch of eggs was removed from the water for a period of one minute twice on Day 3 and thereafter twice a day until the end of Day 6, when each batch was removed and the hatched and unhatched eggs counted under the binocular dissecting microscope. The papers bearing the eggs were then replaced in their tubes, which had in the meantime been filled with BHY. Any remaining unhatched eggs

---

* When the paper is removed from the water the eggs are still wet and it is possible that the stimulus is in fact a dropping temperature resulting from evaporation from the egg surfaces. Hatching occurs in a proportion of the eggs on return to water.

TABLE VI.

Effect of number of matings of the female parent on the hatching-response of eggs of *A. aegypti* during a period of 6 days from time of laying. Eggs submerged on day of laying and exposed to air for 1 minute twice daily from Day 3 to Day 6.

No. matings	1				2								4	6	10													15	
No. of eggs	8	22	42	28	36	30	23	53	16	13	14	45	36	24	17	23	21	56	32	19	35	36	57	18	28	17	19	27	11
Day 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
,, 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
,, 3–	— 4	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —	— —
,, 4–	1 1	— 1	— 1	— 1	— 25	— 1	— —	— —	— —	1 9	— —	4 20	— —	— —	4 4	— —	— —	— 3	1 1	— —	— 14	— 1	— 1	— —	— —	— —	— —	— —	— —
,, 5–	1 —	— —	— 1	1 1	— —	1 3	— —	10 5	— —	— —	— —	— 3	10 8	— —	— —	— —	— 1	33 1	1 2	— 1	2 12	— —	10 5	— 1	3 —	4 1	— —	— —	— 2
,, 6–	— —	2 —	— 8	— 2	— —	— —	— —	— —	— —	— 1	— —	— —	— —	— —	— —	— —	— —	— 3	— 2	— —	— —	1 —	— —	— —	— —	— —	— —	— 1	— —
,, 7*	1	19	32	23	11	25	23	38	16	2	14	18	18	24	9	23	20	16	25	18	7	34	41	17	25	12	19	26	9
Proportion hatched by end of Day 6	0·88	0·14	0·24	0·18	0·69	0·17	0	0·28	0	0·85	0	0·60	0·50	0	0·47	0	0·05	0·71	0·22	0·05	0·80	0·06	0·28	0·06	0·11	0·29	0	0·04	0·18

The upper entry for Days 3–6 represents the number of eggs which hatched before the application of the exposure-stimulus.

* All unhatched eggs treated with BHY at end of Day 6.

hatched within 15 minutes of being introduced into this medium. The stimulus of a minute's exposure to air twice daily from Day 3 up to and including Day 6 resulted in larger hatches than with simple cold treatment, but even so there were certain batches which remained wholly or partially refractory to treatment. The results are shown in Table VI. The proportion of eggs hatching in each batch before treatment with BHY is shown at the bottom of the Table and it will be seen that response to the stimulus of one minute's exposure to air between Day 3 and Day 6 varies from batch to batch. but bears no relation to the number of matings. On the other hand, the response to BHY on Day 6 is uniform, irrespective of the number of matings.

Summary.

Eggs of *Aëdes* do not necessarily hatch on becoming mature, even though conditions are known to be compatible with hatching. Even the eggs laid by a single female in a single batch and kept submerged in a single container may hatch in instalments over a very long period and, although on one occasion a high proportion of the eggs may hatch within a given period, on another, for no apparent reason, very few may hatch.

The problem of erratic hatching has been studied here mainly in *Aëdes africanus* (Theo.) and *A. aegypti* (L.). It is considered that mature eggs enter a state of diapause, the depth of which varies with the passage of time, and that the manner of this variation with time itself varies from egg to egg. Different batches of eggs laid by females of the same species vary in the proportion of the different kinds of egg present.

Variation in response of the eggs has been studied by the application of a suitable hatching-stimulus in equal daily doses. The stimulus used was sufficiently weak to allow variation in response to be manifested, but sufficiently strong to outweigh uncontrolled variables in the environment.

Tests were made of certain variables which occur between females and between the eggs laid in a single batch, and which might conceivably influence the hatching-response of the eggs. It was shown that the following may be excluded as having any influence on the subsequent hatching-response of the eggs: the orientation of the eggs with respect to gravity; small differences in age at the time of submergence; the order in which the eggs in a batch are laid; the number of blood-meals taken by the mother during pregnancy and the number of matings by the mother before the first blood meal. Inconclusive results were obtained about the influence of the amount of some hypothetical substance laid with the eggs by the mother.

It is suggested that variation in the hatching-response of *Aëdes* eggs has an inherited basis.

References.

Bacot, A. W. (1916). Report of the entomological investigation undertaken for the Commission for the year, August 1914 to July 1915.—Rep. Yell. Fev. Comm., **3,** pp. 1–191.

Bates, M. & Roca-Garcia, M. (1945). Laboratory studies of the saimiri-*Haemagogus* cycle of jungle yellow fever.—Amer. J. trop. Med., **25,** pp. 203–216.

Buxton, P. A. & Hopkins, G. H. E. (1927). Researches in Polynesia and Melanesia . . . Parts I–IV.—Mem. Lond. Sch. Hyg. trop. Med., no. 1, 260 pp.

Christophers, Sir S. R. (1945). Structure of the *Culex* egg and egg-raft in relation to function (Diptera).—Trans. R. ent. Soc. Lond., **95,** pp. 25–34.

FIELDING, J. W. (1919). Notes on the bionomics of *Stegomyia fasciata*, Fabr. (Part I).—Ann. trop. Med. Parasit. **13,** pp. 259–296.

GILLETT, J. D. (1951). The larva, pupa and adult male of *Aëdes* (*Stegomyia*) *ruwenzori* Haddow and van Someren (Diptera: Culicidae).—Ann. trop. Med. Parasit., **45,** pp. 195–198.

GILLETT, J. D. (1955). The inherited basis of variation in the hatching response of *Aëdes* eggs (Diptera: Culicidae).—Bull. ent. Res., **46,** pp. 255–265.

HASLAM, J. F. C. (1927). Is there a general factor tending to cause eggs of *Aëdes variegatus* in different experimental pots to hatch on certain days?—Mem. Lond. Sch. Hyg. trop. Med., no. 1, pp. 238–240.

HEAL, R. E. & PERGRIN, M. M. (1945). A technique for the laboratory rearing of *Anopheles quadrimaculatus* Say.—Proc. N.J. Mosq. Ext. Ass., **32,** pp. 105–112.

ROSS, R. W. & GILLETT, J. D. (1950). The cyclical transmission of yellow fever virus through the Grivet Monkey, *Cercopithecus aethiops centralis* Neumann, and the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald.—Ann. trop. Med. Parasit., **44,** pp. 351–356.

YOUNG, C. J. (1922). Notes on the bionomics of *Stegomyia calopus*, Meigen, in Brazil. Part I.—Ann. trop. Med. Parasit., **16,** pp. 389–406.

THE INHERITED BASIS OF VARIATION IN THE HATCHING-RESPONSE OF *AËDES* EGGS (DIPTERA: CULICIDAE).

By J. D. Gillett

East African Virus Research Institute, Entebbe, Uganda.

Eggs of many species of *Aëdes* do not necessarily hatch as soon as they become mature, even though conditions are known to be compatible with hatching. These eggs enter a state of diapause, the depth of which varies with the passage of time in any one egg and the manner of this variation with time itself varies from one egg to another (Gillett, 1955). It seems that, at least in *Aëdes* (*Stegomyia*) *africanus* (Theo.) and in *A.* (*S.*) *aegypti* (L.), variation in the hatching-response is controlled by a property which is quantitatively variable, and is distributed unevenly, not only between batches of eggs laid by different females of the same species, but between the eggs laid by a single female and kept in a single container. Obvious sources of variation, other than genetic, occurring between females and between the eggs laid by a single female have been studied and can be excluded as contributing to variation in the hatching-response of the eggs (Gillett, *op. cit.*). It is the purpose of the present paper to describe an investigation into the possibility that this variation in the hatching-response is inherited.

Terms, Materials and Methods.

Terms. The terms *maturity*, *diapause* and *batch-variation* have been previously defined (Gillett, *op. cit.*); they will be used in the same way here. Two additional terms, *responders* and *non-responders*, will be defined later in this section.

Mosquitos. As it was essential to use mosquitos which would mate readily in captivity, *A. aegypti* was the only species used. Two laboratory colonies of this species were available: one started in 1947 from eggs sent from Nigeria, West Africa, by Dr. J. C. Bugher (Population W); the other started in March 1953, from eggs collected in Tanganyika, East Africa, by members of the Institute staff (Population E). Except where otherwise stated, the mosquitos used were taken from Population W.

Stimuli. A stimulus is necessary for the hatching of *Aëdes* eggs, but different stimuli vary in their effectiveness; strong stimuli induce hatching in a high proportion of mature eggs, weak stimuli induce hatching in only a low proportion. Variation in the hatching-response between batches and between the eggs in a single batch can be studied by the regular application of an easily reproducible stimulus. It is essential, however, to choose a stimulus which is of moderate potency for the species used, in order to allow variation of response to be manifest. Viability of unhatched eggs can be tested later by subjecting them to a maximal stimulus for the species, *i.e.*, a stimulus resulting in the hatching of all unhatched mature eggs. In the previous work, referred to above, it was shown that removal of mature eggs from the water for one minute acted as a suitable moderate stimulus for the eggs of *A. aegypti* and that water containing brain-heart infusion and brewers' yeast (BHY) acted as a maximal stimulus for this species. In the present work, the regular application of the former stimulus was used to demonstrate variation in response and the latter stimulus was used to test for viability in those eggs which had proved refractory to the previous treatment. A few eggs failed to respond to BHY treatment, but these were shown by dissection to be empty and are excluded from the figures in the Tables.

General methods. Female mosquitos (picked out as pupae) were mated individually to known males and given a blood-meal on the writer. Three days later they were transferred to the laying-tubes (Gillett, *op. cit.*), where each laid a batch of eggs on the moist filter paper in the tube. On the day of laying (referred to as Day 0), when the eggs were known to be less than 16 hours old, the pieces of moist filter paper bearing the eggs were introduced into sterile tubes containing 7 ml. tap-water. At Entebbe, where room temperature remains fairly constant at 22–26°C., development of the embryo takes 4–3 days. On the morning of Day 3, the filter paper bearing the eggs was removed from each tube in turn for exactly one minute. During this period, any hatched larvae were removed and counted, and the paper was then returned to the tube, which had in the meantime been refilled with tap-water. Thus all tubes received the same amount of manipulative treatment, whether hatching had occurred or not. This procedure was repeated in the evening, so that every batch of eggs was removed from the water for a period of one minute twice on Day 3 and thereafter twice a day until the evening of Day 6, when each batch was removed and the hatched and unhatched eggs were counted under a binocular dissecting microscope. The papers bearing the eggs were then replaced in their tubes, which had in the meantime been filled with BHY medium.

After maturity of the embryos is reached, the different eggs in a single batch may respond to a moderate stimulus, applied in equal daily doses, at intervals over a very long period. This heterogeneity of response of the eggs in a single batch complicates the picture, but by cutting down the time for each experiment to only four days following embryonic maturity, it becomes possible to neglect intra-batch variation and to regard the eggs simply as *responders* or *non-responders*, the former referring to the eggs in a batch which have responded to treatment applied twice daily from Day 3 up to and including Day 6, the latter, to those viable eggs in the same batch which have failed to respond to identical and simultaneous treatment during that period. Thus, the hatching-response in any egg can be regarded as an all-or-nothing reaction to the particular stimulus, and inter-batch variation here concerns only differences in the proportion of responders present in different batches. This is, of course, an over-simplification, as no regard is paid to the actual time when the eggs respond during the short experimental period. As all the non-responders are brought out by BHY treatment at the end of Day 6, it has been possible to breed both from responders and non-responders.

Experimental.

After a single mating, a female mosquito may lay several batches of eggs following successive blood-meals. If the hatching-response of the eggs is inherited, one would expect to find a similar response (measured as the proportion of responders) in each batch of eggs laid by a single female following a single mating.

Fourteen female *A. aegypti* were mated to a single male each and given a single blood-meal. The batches of eggs derived from these insects were put up in the way described, the pieces of paper bearing the eggs being removed from the water in the tubes for one minute twice daily from Days 3–6. After oviposition, the mother was allowed a second blood-meal and the second brood of eggs was treated in exactly the same way. The results are shown in Table I. With one exception, there is no significant difference between the response of the first and second broods laid by a female following a single mating. On the other hand, there is a highly significant difference between batches laid by different mosquitos, and what has previously been described as inter-batch variation appears to be a manifestation of *inter-mosquito* variation.

TABLE I.

Proportion of responders in two broods of eggs of *A. aegypti* laid by the same mother after a single mating.

♀ No.	First brood	Second brood	χ^2	P	Total
1194	1/20	0/18	—	—	1/38
1188	5/61	0/42	2·06*	0·16	5/103
1199	6/62	3/43	0·02*	0·89	9/105
1166	6/34	1/25	1·43*	0·23	7/59
1190	13/68	2/23	0·70*	0·40	15/91
1154	1/19	14/65	1·66*	0·20	15/84
1170	5/35	16/62	1·75	0·18	21/97
1144	8/17	7/32	3·13	0·08	15/49
1122	10/34	19/57	0·25	0·62	29/91
1168	14/49	22/61	0·69	0·41	36/110
1180	11/28	5/9	0·22*	0·64	16/37
1181	28/38	0/8	12·13*	<0·001	28/46
1179	31/37	54/68	0·30	0·58	85/105
1124	26/30	37/40	—	—	63/70
Total	165/532	180/553			345/1085
	31%	33%			32%
χ^2	0·29				354·79
n	1				13
P	0·59				<0·001

* = Yates' correction applied.

χ^2 not calculated for the first and last entry because the number of responders (or non-responders) was less than 5 in each brood.

The results of this experiment suggest that the response of the eggs is determined by one or both parents. If the male parent contributes to the hatching-behaviour of the eggs then one might expect to find a difference in the proportion of responders in some of the second-brood batches if the female were allowed to mate with a different male between the laying of the two batches. Batches of eggs were obtained from 20 females which had been mated to known males. Each female was then allowed to mate with a new male before feeding for the second time and laying a second batch of eggs. The results are shown in Table II.

It is by no means certain that the second mating is always effective, although effective matings have been obtained following the laying of a sterile batch of eggs. In fact, effective matings have been obtained at all stages of the ovarian cycle, even following the blood-meal and only a day before the eggs are laid, and even between males and females which are over two weeks old. The results of the experiment, however, taken in conjunction with the figures given in Table I, suggest that the hatching-behaviour of the eggs is at least partly determined by the male parent; half the cases show a significant change in the proportion of responders. Absence of change in the other half may be attributable to chance selection of the second male, but ineffectual second matings cannot be wholly excluded.

The next step was to find out what part, if any, the female parent plays. If she contributes nothing to egg-response then different females mated to the same male should show no significant difference between their respective egg-batches.

TABLE II.

Proportion of responders in two successive broods of eggs of *A. aegypti* laid by the same mother after mating with different males.

♀ No.	First brood	Second brood	χ^2	P
1138	7/8	2/12	7·08*	0·008
1139	25/36	0/28	29·06*	<0·001
1151	12/32	1/35	12·24*	<0·001
1268	14/22	26/68	4·34	0·04
1269	26/81	43/61	20·53	<0·001
1270	26/35	44/89	6·31	0·01
1272	33/55	17/63	13·11	<0·001
1282	4/40	10/29	4·81*	0·03
1289	50/80	23/76	16·27	<0·001
1339	2/27	27/62	9·60*	0·002
1342	32/66	5/53	20·92	<0·001
1273	35/67	17/42	1·43	0·24
1276	17/30	51/68	3·29	0·07
1278	31/34	13/19	3·01*	0·08
1279	26/63	14/34	0·00008	>0·99
1281	11/43	17/37	3·63	0·06
1287	1/29	5/37	0·96	0·33
1288	8/52	8/77	0·71	0·40
1291	9/49	5/29	0·016	0·89
1352	39/64	26/59	3·51	0·06

* = Yates' correction applied.

Twenty male *A. aegypti* were mated to two females each and batches of eggs were obtained from each of these females and treated in the way described above. The results are set out in Table III. Again, about half the cases show a significant change in the proportion of responders. This is the type of result which would be expected if " good " males are mating with " good " and " bad " females, and " bad " males with " good " and " bad " females. Since changing the male or changing the female alters the overall batch behaviour it would seem that both parents contribute something to the hatching-behaviour of the eggs.

The results so far were all compatible with the view that the hatching-behaviour of the eggs is inherited, and it seemed reasonable to attempt selective breeding of responders and non-responders. The apparently quantitative nature of the variable controlling the hatching-response would not lead one to expect that selection would result in clear-cut segregation into wholly responder or non-responder classes, but it might result in an increased homogeneity of response in one direction or the other. Many such attempts were made but all failed on account of certain unforeseen difficulties. After several generations in the " lines " selected for responders it became increasingly difficult to induce the mosquitos to mate. In the " lines " selected for non-responders, the difficulties with mating were not so great but by the sixth generation many of the females, although successfully mated and fed, failed to develop eggs, even when given a second or third blood-meal.

Mating in these experiments was confined to batch-mates and it seems likely that the difficulties encountered can be attributed to close inbreeding. It was considered that, by regular out-breeding, some of these difficulties might be avoided and it was planned to make a further attempt at selection using *A.* *aegypti* both from the old colony (Population W) and from the new colony (Population E). It was necessary, however, to keep Populations W and E separate for the first generation in order to see if the eggs from Population E exhibited comparable behaviour. The results were unexpected (Table IV): the proportion of responders in the 12 batches of eggs laid by the new E-adults was very high (46–100%), while in the 14 batches of eggs laid by the W-adults it was unexpectedly and uniformly low (0–9%). The original plan of combining these two populations in a further attempt at increasing homogeneity of response by selection was, therefore, abandoned in favour of using these two populations, in which a high degree of homogeneity of response was already present, for purposes of comparison and crossing.

TABLE III.

Proportion of responders in eggs of *A. aegypti* laid by two different females mated with the same male.

1st female	2nd female	χ^2	P
4/40	10/42	1·87*	0·17
21/100	40/56	38·34	<0·001
16/61	23/98	0·15	0·70
1/36	23/83	8·21*	0·004
2/59	1/27	—	—
12/32	28/35	12·74	<0·001
0/16	1/19	—	—
63/79	24/106	59·25	<0·001
85/105	16/37	18·94	<0·001
7/60	5/103	2·58	0·11
21/114	8/95	4·34	0·04
14/22	26/81	7·24	0·007
35/67	37/48	7·37	0·007
26/63	11/43	2·77	0·09
41/66	50/80	0·002	0·96
3/51	8/52	1·54*	0·22
4/50	1/29	—	—
9/49	5/15	1·51	0·22
18/71	11/36	0·33	0·57
36/58	2/21	21·62*	<0·001

* = Yates' correction applied.

χ^2 not calculated for those groups where the numbers were very small and where there is obviously no significant difference.

Some of the adults derived from the responders of Population E were mated together, and some of the adults derived from the non-responders of Population W were mated together, care being taken in both groups to avoid mating between batch-mates. The eggs laid by these were treated in the usual way with the results shown in Table V. The new generation of Population E and the new generation of Population W were run simultaneously and under conditions identical in every way. It can be seen by comparing the results shown in Tables IV and V that homogeneity of response in these two populations was preserved from one generation to the next (Population E, 46–100 and 65–100%; Population W, 0–9 and 0–11%).

TABLE IV.

Proportion of responders in eggs of two populations of *A. aegypti*.

POPULATION W			POPULATION E		
Batch No.	Proportion of responders	%	Batch No.	Proportion of responders	%
1392	4/16	—	1404	61/61	100
1389	2/13	—	1405	39/39	100
1400	3/34	9	1408	48/49	98
1384	4/63	6	1403	42/43	98
1388	2/34	6	1401	58/60	97
1385	1/42	2	1411	55/57	97
1381	0/50	0	1409	41/47	87
1383	0/44	0	1412	6/7	—
1395	0/37	0	1406	41/52	79
1382	0/31	0	1402	50/67	75
1390	0/24	0	1407	27/51	53
1394	0/20	0	1410	19/41	46
1387	0/9	—			
1391	0/9	—			
Total	16/426	3·8		487/574	84·4

Percentage of responders not calculated when the total number of eggs in a batch was less than 20.

The remainder of the new generation from both populations was used for reciprocal crosses between adults derived from non-responders of Population W and responders of Population E. Batches of eggs were obtained from 14 W × E crosses and from 17 E × W crosses and the results are shown in Table VI.

TABLE V.

Proportion of responders in eggs laid by adults of *A. aegypti* derived from the non-responding and the responding eggs of Populations W and E respectively.

POPULATION W			POPULATION E		
Batch No.	Proportion of responders	%	Batch No.	Proportion of responders	%
1457	2/12	—	1435	68/68	100
1447	5/45	11	1439	32/32	100
1459	2/19	—	1430	18/18	—
1449	4/58	7	1431	4/4	—
1443	3/46	7	1428	62/63	98
1445	4/64	6	1433	40/41	98
1448	2/35	6	1434	36/37	97
1452	2/37	5	1432	32/33	97
1450	4/76	5	1438	26/27	96
1454	2/42	5	1425	32/34	94
1446	2/47	4	1436	69/81	85
1444	1/35	3	1426	53/63	84
1451	1/68	2	1429	51/67	76
1453	0/52	0	1437	51/68	75
1456	0/11	—	1427	33/51	65
Total	34/647	5·3		607/687	88·4

Percentage of responders not calculated when the total number of eggs in a batch was less than 20.

It is clear that whichever way the cross is made, homogeneity of response is lost (W × E, 16–100%; E × W, 4–99%), and considerable support is added to the view that both parents contribute to the hatching-behaviour of the eggs. The experiment recorded in Table V may be taken as the control for that recorded in Table VI, as the two were done simultaneously, in the same place and under precisely the same conditions.

TABLE VI.

Proportion of responders in eggs from reciprocal crosses between Populations W and E of *A. aegypti*.
W—adults derived from non-responding eggs, E—adults derived from responding eggs.

W ♂♂ x E ♀♀			E ♂♂ x W ♀♀		
Batch No.	Proportion of responders	%	Batch No.	Proportion of responders	%
1467	67/67	100	1482	67/68	99
1471	17/17	—	1483	76/83	92
1464	35/36	97	1490	53/66	80
1466	51/53	96	1493	57/73	78
1468	38/41	93	1492	14/18	—
1475	44/51	86	1481	18/26	69
1470	31/36	86	1494	46/71	65
1463	34/56	61	1489	31/52	60
1465	26/43	61	1488	20/34	59
1476	3/5	—	1486	24/41	59
1472	7/18	—	1491	19/36	53
1474	20/65	31	1495	9/19	—
1473	6/38	16	1498	19/42	45
1469	0/12	—	1484	19/45	42
			1487	20/61	33
			1485	10/68	15
			1496	1/27	4
Total	379/538	70·5		503/830	60·6

Percentage of responders not calculated when the total number of eggs in a batch was less than 20.

From Table IV it will be noted that 487 out of the 574 E-eggs responded during the four days' treatment. Some of the adults derived from the 87 non-responders were mated together (care being taken to avoid matings between batch-mates) and set up in a similar experiment at the same time and under the same conditions as those reported above. The results are shown in Table VII and indicate that selection of non-responders, even from a population (such as E) that has a characteristically high proportion of responders, resulted in a lowering of the range of the proportion of responders (27–64%) as compared with the range found in those selected from the responders (65–100%).

Discussion.

The experiments reported in this paper indicate that the hatching-behaviour of the eggs of *A. aegypti* is mainly controlled by an inherited property. It would appear that quantitative factors contributed by both parents determine the depth of diapause in an egg and its changes of depth with the passage of time. That the depth of diapause may vary within very wide limits in the eggs of a single batch leads one to suspect that a multiple-factor mechanism is involved. Nevertheless, batch-homogeneity has been recorded occasionally and was especially marked in the population of *A. aegypti* recently colonised from Tanganyika (Population E). Scope for variation may be enormously increased by the possibility of previous matings by the mother with more than one male; it has been shown that, in captivity, a single female *A. aegypti* may mate as many as 40 times before her first blood-meal (Gillett, *op. cit.*).

TABLE VII.

Proportion of responders in eggs of *A. aegypti* adults derived from the non-responding eggs of Population E.

Batch No.	Proportion of responders	%
1506	32/50	64
1510	13/24	54
1508	17/34	50
1501	19/39	49
1509	12/25	48
1507	13/36	36
1503	5/15	—
1505	7/22	32
1502	6/22	27
1504	3/19	—
Total	127/286	44·4

Percentage of responders not calculated when the total number of eggs in a batch was less than 20.

A variable delay in the hatching of eggs is advantageous to a species living during its aquatic stages in temporary collections of water. But two different geographical populations of *A. aegypti* have been shown here to exhibit different behaviour: in one (W) a variable delay in hatching was usual; in the other (E), most of the hatching occurred soon after the eggs had reached maturity. It must be emphasised that both populations, whatever their origin, were laboratory colonies. In the maintenance of these colonies all the eggs laid are preserved for a prolonged period and all are finally hatched on introduction to a medium containing a strong hatching stimulus. Population W had been maintained as a colony since 1947 and thus, over a period of six years, there had been no selection either for responders or non-responders. This does not exclude the possibility that during this period there may have been random loss and fixation of genes resulting from the limited size of the original sample of eggs from West Africa and the artificial limits of size imposed on the colony thereafter. Nevertheless, in all but the last experiment, adult mosquitos derived from pupae picked at random from this colony have produced egg-batches with a characteristic high heterogeneity of response. Unless the genetic makeup of this population had changed rather suddenly between April and September 1953, it is difficult to account for the very high proportion of non-responders in the apparently random sample that was used in the last experiments comparing the behaviour of the two populations. It was, in fact, this sudden change towards increased homogeneity of response in Population W that made the crossing experiments possible. Population E had been maintained as a colony for only five months when the sample was tested and found to contain such a high proportion of quick responders. Now, a high proportion of slow responders, as was found in the sample from Population W, would not necessarily be disadvantageous to a species spending its aquatic stages in small artificial containers of water subject to continual emptying and refilling. But a high proportion of quick responders, as was found in Population E, would surely be disadvantageous, as all the larvae would tend to be lost through emptying and drying of the water containers. Can this inherited difference in the behaviour of the eggs between these two populations be associated with other differences in behaviour or with possible differences in the environment?

Female *A. aegypti* of Population W usually lay all or most of their eggs in one sitting and thus all would be lost if simultaneous hatching occurred just before the container became dry. For example, in these experiments, of the 46 W-females which laid eggs, only eight did not deposit all the eggs in a single sitting. None of these eight laid more than two sub-batches and four of them laid their eggs on two consecutive days and may have been interrupted during a brief lull in laying, and thus had the division into two sub-batches artificially imposed on them. The other four laid the bulk of their eggs in a single sitting but laid one, two or four more eggs only, a few days later. By contrast, of the 41 E-females which laid eggs, 16 laid their eggs in more than one sitting, many of them laying their eggs in a series of small sub-batches over a number of days. For example, E-female No. 1465 laid as many as six sub-batches over a period of nine days, consisting of 11, 3, 2, 3, 4 and 20 eggs. Thus it is probably true to say that in Population W the eggs are usually laid in a single sitting but hatching of the eggs is erratic and scattered over a considerable period of time, while in Population E, egg-laying is prolonged over a number of days but hatching of the eggs mostly occurs together over a short period of time. While in Population W survival is ensured, should a water container become dry, by the erratic hatching-response of the eggs, the chances of survival in Population E are increased by the habit of the females in laying their eggs in small sub-batches over a number of days. It is clear that this habit must tend to result in the eggs being laid in a number of different containers and that scattering in time automatically results in scattering in place.

Newala, Tanganyika, the original home of Population E, is a dry, isolated plateau. Water is at a premium in such a place and the local human population has reacted by storing it in large pots sunk into the floors of their houses (W. H. R. Lumsden, personal communication). These pots form semi-permanent reservoirs and it may be that selection pressure for heterogeneity of response of the eggs has been less than in other regions, and has allowed the building up of a quick-responder race. In this connection it is interesting to note that, at Entebbe, embryonic development in Population E takes about 12 hours less than in Population W. It is possible that the difference in environment has resulted in selection for scattered laying rather than scattered hatching. It seems reasonable to suppose that the Newala population of *A. aegypti* is more or less cut off from other populations of the same species. It is possible, therefore, that homogeneity of the material has resulted in the first place from the chance introduction of a few individuals which showed a low degree of variability and the maintenance of homogeneity by the absence of selection pressure and perhaps the random loss and fixation of genes. The adults of Population E were somewhat paler than those of Population W; about 2 per cent. of them were very pale indeed, the scutum being pale straw coloured, but these very pale forms were not used in the experiments.

Delayed or erratic hatching has been noted in different subgenera of *Aëdes*: in *Stegomyia* by Atkin & Bacot (1917) and many others, in *Ochlerotatus* by Marshall (1938) and others, in *Aëdimorphus* by Gjullin, Yates & Stage (1939) and others, in *Aëdes* and *Finlaya* by Gjullin, Hegarty & Bollen (1941) and in

Banksinella by Gillett (*op. cit.*). Although the phenomenon appears to be widespread in the genus, the actual details of hatching-behaviour vary very much from species to species. It has been shown here that clear-cut differences in behaviour may occur between two populations of the same species and that variability may be reduced. While a decrease in variability may perhaps be associated with the limited size of a population, the direction which this decrease of variability takes may be partly decided by selection and maintained by geographical isolation. An inherited difference of behaviour between two populations of the same species can clearly be a step towards speciation, and it seems probable that in some instances selection has favoured deep diapause for prolonged periods and in others, a shallow diapause of shorter duration; while in yet other instances a highly heterozygous state has resulted which ensures maximum variation in response in each batch of eggs laid.

Summary.

A stimulus is necessary for the hatching of eggs of *Aëdes* mosquitos, but, while many different kinds of change in the external environment may be adequate as hatching-stimuli, there is variation in the response of the eggs to any given one of them.

Not only is there variation between species as regards behaviour of the eggs, but batches of eggs laid by different females in a single species may vary one from another and there is even variation of behaviour between the eggs laid in a single batch.

The response of the eggs of *A. aegypti* (L.) has been studied here and evidence produced that both parents contribute to their hatching-behaviour. Egg behaviour has also been studied in two populations of this species, one originating from West Africa and the other from East Africa. In the former, only a very low proportion of the mature eggs (0–9%) responded to the daily application of a suitable stimulus over a short period, whereas in the latter the proportion of responders in the same period with the same stimulus was very much higher (46–100%). The next generation reared from each of these gave very similar results (0–11 and 65–100%, respectively), while reciprocal crosses between them gave a wide range of scatter (16–100 and 4–99%, respectively).

It is concluded that hatching-behaviour of the eggs in *A. aegypti* is mainly inherited. It appears that the mature eggs enter a state of diapause, the depth of the diapause and its changes with time being determined by factors contributed by both parents.

The advantages of variation in response to a hatching-stimulus are pointed out. Delayed or erratic hatching is widespread in the genus and it seems probable that similar mechanisms are involved, actual differences in hatching-behaviour between populations or between species being determined by isolation and selection.

References.

Atkin, E. E. & Bacot, A. (1917). The relation between the hatching of the eggs and the development of the larvae of *Stegomyia fasciata* (*Aëdes calopus*), and the presence of bacteria and yeasts.—Parasitology, **9,** pp. 482–536.

Gillett, J. D. (1955). Variation in the hatching response of *Aëdes* eggs (Diptera: Culicidae).—Bull. ent. Res., **46,** pp. 241–254.

Gjullin, C. M., Hegarty, C. P. & Bollen, W. B. (1941). The necessity of a low oxygen concentration for the hatching of *Aëdes* mosquito eggs.—J. cell. comp. Physiol., **17,** pp. 193–202.

Gjullin, C. M., Yates, W. W. & Stage, H. H. (1939). The effect of certain chemicals on the hatching of mosquito eggs.—Science, **89**, pp. 539–540.

Marshall, J. F. (1938). The British mosquitoes.—341 pp. London, Brit. Mus. (Nat. Hist.).

THREE NEW COCCIDS (HEMIPT.: COCCOIDEA) ATTACKING COFFEE IN EAST AFRICA.

By G. De Lotto

5 H

Department of Agriculture, Kenya.

Three insects of interest or importance on coffee in East Africa are dealt with in this paper. For a considerable time it has been realised that the identity of the common *Ceroplastes* on coffee in Kenya was in doubt, and the necessity for this to be cleared up has arisen through the interest shown by Australian workers in the insect as a host from which parasites might be obtained for introduction against *Ceroplastes destructor* Newst. in that country. Gurney, reporting on his visit to East Africa to collect parasites of *C. destructor* as long ago as 1935–36, suspected that more than one white waxy scale was involved on coffee plants in these territories, as some of the parasites obtained failed to attack the Australian scale (Gurney, 1936).

For this study, therefore, specimens of two species of *Ceroplastes* were obtained from Australia, two from Uganda, and two from Kenya, these latter two including the common coffee insect concerning the identity of which there had been doubt.

One of the species from Australia appeared to be correctly identified as *Ceroplastes ceriferus* (And.) and as this insect does not occur in East Africa it need not be referred to again. The other species from Australia, labelled *Ceroplastes destructor* Newst. was very carefully examined and found to be identical with a species of *Ceroplastes* obtained on *Gymnosporia* sp. in Nairobi. These were all compared with specimens from the collection of the Department of Agriculture, Uganda, labelled " No. 467—*Ceroplastes ceriferus* (And.), Entebbe 3.ii.1910 " indicating that they belong to a second lot of material, collected by C. C. Gowdey and forwarded to Newstead for identification (Newstead, 1910) and later recognised by him as *C. destructor* (Newstead, 1917). Although fully mature and moderately chitinised, no noticeable differences were found, except that the colour of the wax test—reduced to a mere fragile pellicle—is golden yellow, whilst in Australian and Kenya specimens the test is white or dirty white. This difference in colour might well be due to the very long period of storage. All three lots are therefore placed as *C. destructor*.

A further species was obtained from Uganda, consisting of fresh specimens collected on *robusta* coffee in January 1954, and supposed to be *C. destructor*. These insects must be referred to *C. brevicauda* Hall (Hall, 1931). This species was described by Hall as a variety of *destructor* Newst. but in the writer's opinion the two insects are so distinct in the shape and size of the caudal process that *C. destructor* var. *brevicauda* is here raised to specific rank. Uganda examples show the outer stigmatic spine somewhat longer and more frequently bifurcate than in Rhodesian material, but in every other respect they are typical.

The remaining species, that from coffee in Kenya, is described below as a new species.

Examination of the material referred to above shows that its practical bearing on parasite collection is as follows:

Ceroplastes ceriferus (And.), Australia, not found in East Africa.

Ceroplastes destructor Newst., present in Australia, Uganda and Kenya (but not found on coffee in Kenya up to the present).

Ceroplastes brevicauda Hall, Uganda, on coffee.
Ceroplastes luteolus, **sp. n.,** Kenya, on coffee.

Ceroplastes luteolus, sp.n. (fig. 1).

Test of the adult female more or less hemispherical with a deep depression along the lateral margin, not divided into plates; centre of the dome with a small elongate pad. Colour evenly light yellow with four bands of opaque white

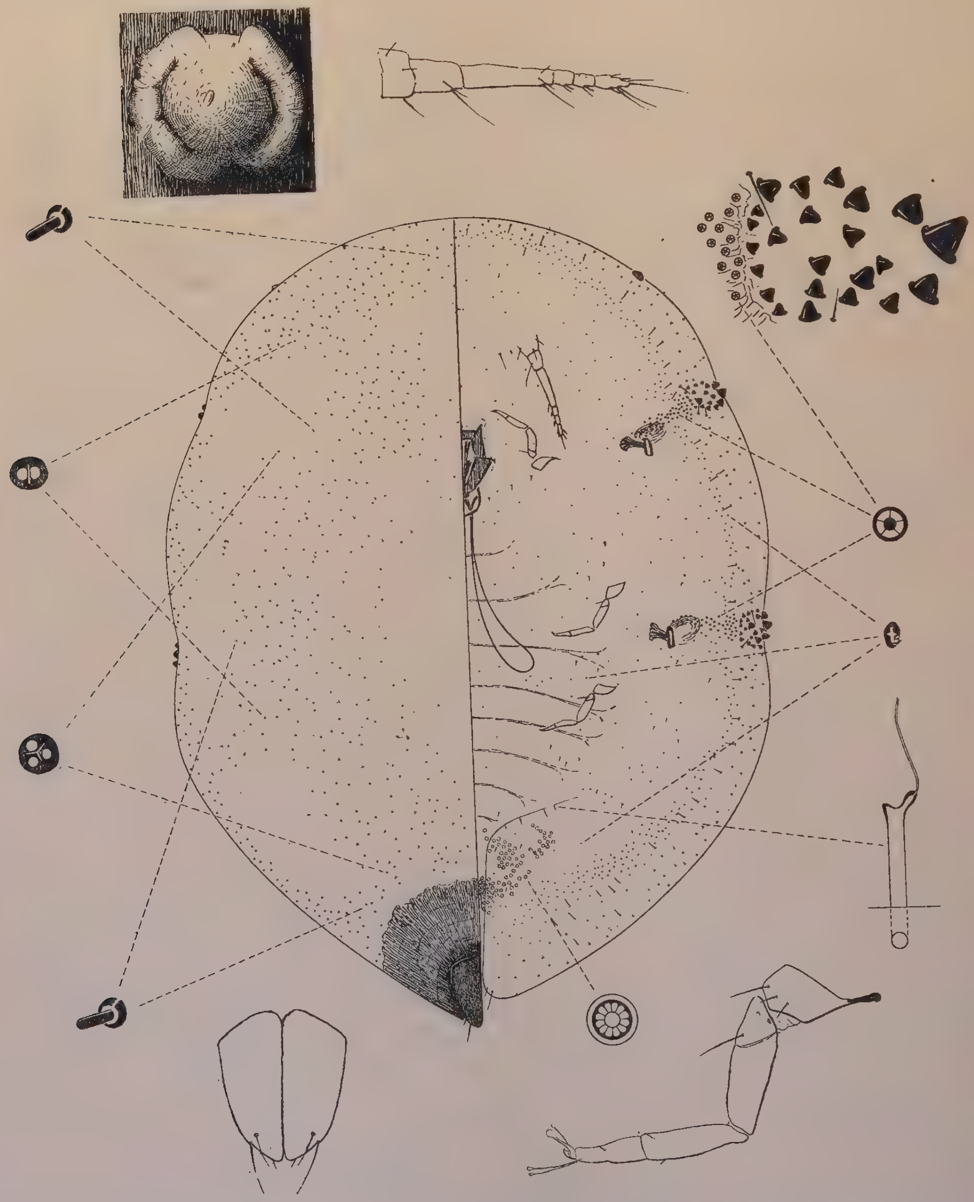


Fig. 1.—*Ceroplastes luteolus*, sp.n

wax arising from the stigmatic clefts; wax rather thick and extremely soft. Length 4 to 6 mm.; breadth 5 to 7 mm.

Denuded of wax the body of the female is hemispherical, devoid of lateral or cephalic tubercles; caudal process very short, conical and strongly chitinised; dermis at full maturity only moderately chitinised. The following morphological details apply to young adult specimens. Antennae well developed, of six segments, the third of which is always the longest, being about one third of the total length. Legs normal with one of the ungual digitules stout and broadly clavate as usual, whilst the other is much thinner and similar to the tarsal digitules, but much shorter. Margin of the body provided with very small setae set widely apart at irregular distances; two large setae of different length are inserted at the apex of each anal lobe. Stigmatic clefts with a group of 19 to 32 conical spines of various size, normally broadly rounded or pointed. A few setae present with each group of stigmatic spines. Anal process very short, and heavily chitinised even in the youngest specimens. Anal plates elongate carrying three setae apically. Ventral dermis with very small elongate glands having a central cruciform orifice. In young individuals these glands tend to be crowded along the margin, forming a continuous irregular line. Ventral setae—except those inserted in the interantennal area—few and minute. Quinquelocular glands associated with the stigmatic openings rather numerous and extending in an irregular row. Multilocular disc pores all around the vulva. Dorsum evenly covered (all but a small area around the stigmatic clefts) by numerous bi- or trilocular glands and very short cylindrical setae.

KENYA: Nairobi, 24.v.1953, 3 mounted ♀♀ collected on branches of *Coffea arabica* (*R. H. Le Pelley*); Nairobi, 16.xi.1953, 8 mounted ♀♀ from *Citrus maxima* (*R. H. Le Pelley*); Nairobi, 17.xii.1953, 2 mounted ♀♀ from *Markhamia platycalyx* (*G. De Lotto*).

The holotype which will be deposited in the British Museum (Natural History), London, is a young adult female in which chitinisation has not yet set in; it was selected from among the specimens collected on coffee. One paratype—also from coffee—will be sent to the U.S. National Collection of Coccidae, Washington, D.C., U.S.A.; the remainder are in the collection of the Department of Agriculture, Nairobi, Kenya.

This species of *Ceroplastes* is rather common in the area of Nairobi where it attacks certain cultivated and wild plants. It was at times erroneously referred to *destructor* which is close to it but easily separable even in living material, as in *destructor* the test is white and much larger. In mounted specimens of *destructor* the outline of the female is elongate and provided with a caudal process about half the length of the body. *C. luteolus* is instead much closer to *brevicauda* but even this insect does not agree with the Kenya species as, although the caudal process is shorter than in typical *destructor*, it is in any case larger than in *luteolus*, and—at least in the specimens at hand—not appreciably more sclerotized than the remaining body dermis. Furthermore, in *brevicauda* the stigmatic spines, as well as the setae associated with them, are more numerous.

An interesting Asterolecaniid from coffee, long known to be new, is also described here. This insect is not a serious pest.

Lecaniodiaspis erratica, sp.n. (fig. 2).

Test of the adult female circular, moderately convex with a small operculum at the anal end; colour light brown, at times darker on the median area. Diameter 2–2·5 mm.

Body circular or a little broader than long, remaining membranous at maturity. Antennae small, divided into three or four ill-marked joints, the last of which carries a cluster of stout setae. The legs are recognisable only in a few specimens as extremely small, rounded or pointed membranous tubercles provided with two or three minute setae distally. Anterior and posterior spiracles well developed and beset by a group of 4 to 8 quinquelocular pores. Stigmatic spines entirely lacking. Anal cleft somewhat chitinised along the margin and carrying a few setae one of which is moderately long. Multilocular disc pores confined to the median region of the posterior abdominal segments and rather numerous about

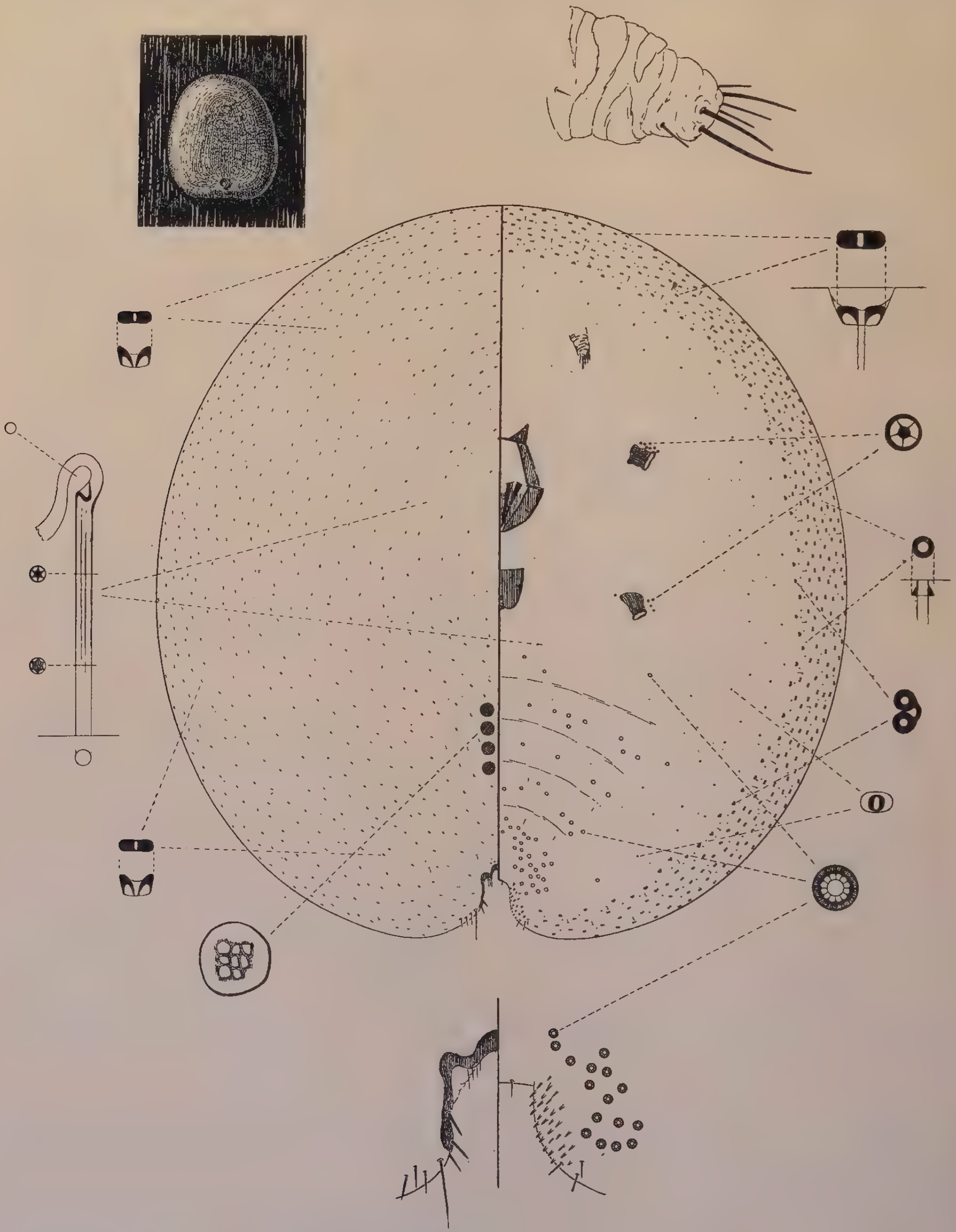


Fig. 2.—*Lecaniodiaspis erratica*, sp.n.

the vulva. Ventral dermis with a continuous band of 8-shaped glands disposed in more or less regular lines along the margin. A few glands referable to the 8-shaped type, but smaller, are scattered over the venter; other still smaller circular glands having a single central opening and a few minute setae are intermixed among the glands of the marginal series. Dorsum with 8-shaped glands of the same shape as those of the ventral marginal series but a little smaller, and evenly distributed all over the surface. Dorsal cribriform plates large and set close to the median line of the body; normally there are eight plates, but occasionally some of them are divided into two or more smaller irregular ones. Long tubular ducts, with the median part somewhat pigmented and divided into six loculi, are very numerous on both surfaces of the body.

KENYA: Nairobi District, Kiambu, 17.vii.1942, 15 mounted ♀♀ collected on stems and branches of *Coffea arabica* (*R. H. Le Pelley*).

The holotype is a young adult female which will, in due course, be deposited at the British Museum (Natural History). As usual a paratype will be presented to the U.S. National Collection of Coccidae, whilst the remaining paratypes are in the collection of the Department of Agriculture, Nairobi, Kenya.

This species was first stated to be new by Dr. H. Morrison who examined specimens sent by Dr. R. H. Le Pelley in 1951. Since the species shows peculiar characters common to both *Cerococcus* and *Lecaniodiaspis*, he suggested the erection of a new genus. The writer while agreeing with this view prefers for the time being to include the species in the genus *Lecaniodiaspis* and to leave the possible erection of a new genus until a critical study of these groups of ASTEROLECANIIDAE, or at least a revision of the small batch of species so far described from the Ethiopian region, is undertaken.

The third species is a mealybug from coffee in Uganda, and this opportunity is taken to describe it, since it has been and may be confused with other mealybugs from coffee.

Pseudococcus latipes, sp. n. (fig. 3).

Living insect not seen.

Body broadly oval, being, in mounted specimens, 2 to 2·8 mm. long, 1·5 to 2·2 mm. wide.

Cerarii, in a complete series of eighteen pairs, each having two robust spines, except the ocular cerarius (xvi) and the three or four cerarii anterior to the anal lobes each of which is provided with up to 5 or 6 spines of various sizes, often associated with 1 to 3 small supplementary setae similar to those of the dorsum. Anal lobe cerarii with but two spines beset by numerous trilocular pores and a few slender setae, and surrounded by an ill-defined sclerotized area. Anal lobes with a well-marked bar ventrally, a long apical seta and a shorter subapical one. Dorsal tubular ducts entirely absent. Ventral ducts small and crowded in three or four groups on the margin of the last segments of the abdomen. Multilocular disc pores on the ventral abdominal area arranged in five or—very seldom—six groups as follows: (iv) 0–2; (v) 9–17; (vi) 16–26; (vii) 36–55; (viii) 39–56; (ix plus x) 28–37. The pores on segments (vii) and (viii) are at times supplemented by a few others scattered on the submarginal area, whilst on segments (iv) to (vi) they are always arranged in a linear row along the distal margin only. Other more or less numerous multilocular disc pores are scattered all over both surfaces of the body, especially along the margin and on the median area of the dorsum. Circular disc pores * generally only a little smaller than the multilocular disc pores. Five to seven groups of these pores occur on the median area of the dorsum; others rather numerous are distributed on the body particularly along the marginal area of the venter. Trilocular pores numerous and evenly distributed. Dorsal setae short, ventral ones longer but slender. Dorsal ostioles large, having their lips somewhat chitinised. Circulus large, oblong, divided transversely and membranous. Legs short and stout, with some translucent pores on the hind coxa and tibia. Antennae eight-jointed.

---

* These circular or disc "pores" which occur in many species of mealybugs were first noticed by Hall in *Pseudococcus njalensis* Laing (Hall, 1945) who remarked that their structure is obscure. It is very probable that they are not true pores but body sensoria.

Uganda: Toro, 21.v.1951, 15 mounted ♀♀ collected on leaves of *Coffea robusta* (*D. J. McCrae*).

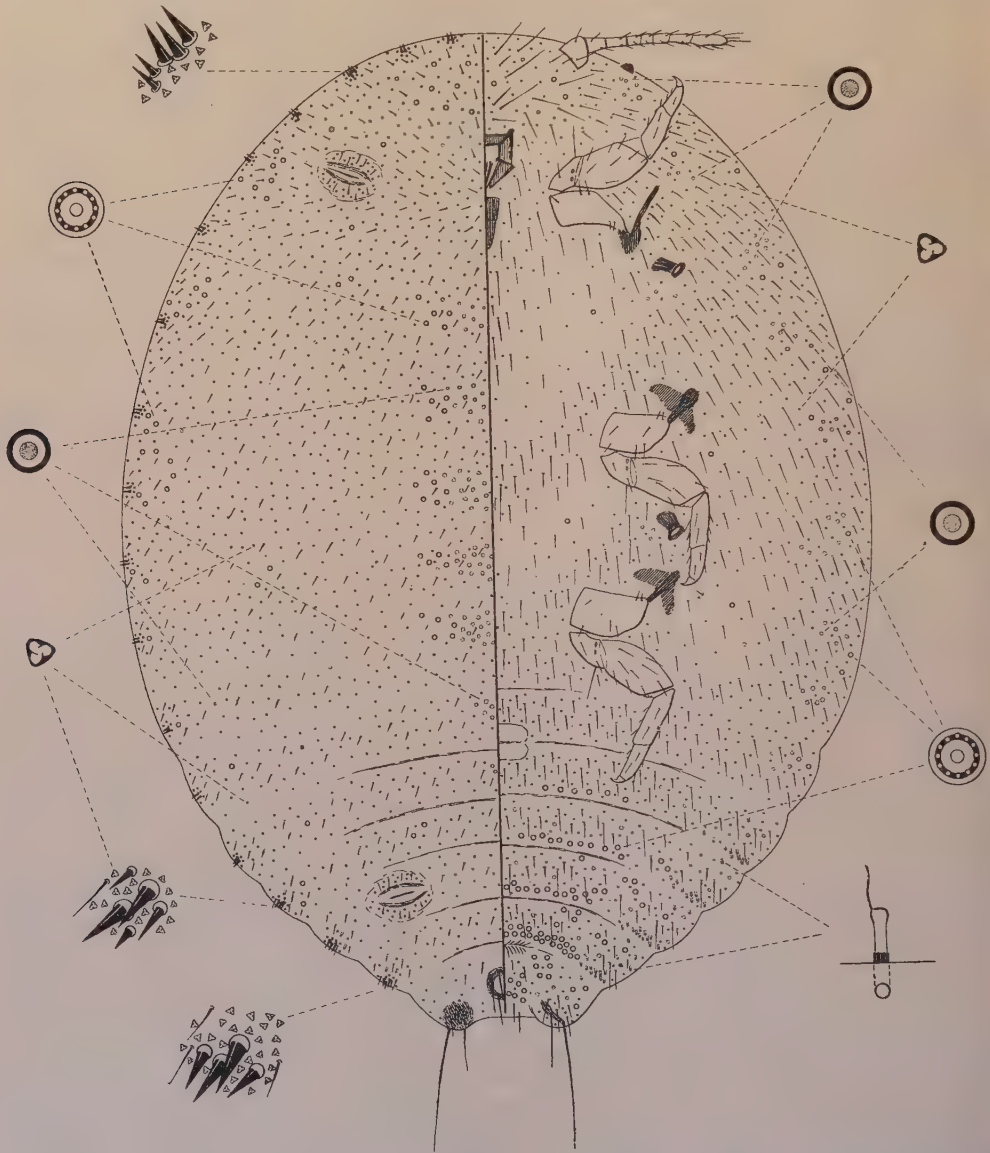


Fig. 3.—*Pseudococcus latipes*, sp.n.

The holotype will be deposited in the British Museum (Natural History) and one paratype in the U.S. National Collection of Coccidae; the remainder are in the collection of the Department of Agriculture, Nairobi, Kenya.

The species described above does not properly fit into any of the genera of PSEUDOCOCCIDAE as conceived or restricted recently by Ferris, and the assignment of the species to the genus *Pseudococcus* must be understood to be a provisional measure to avoid the erection of a new genus, since this will be best left until the PSEUDOCOCCIDAE of Africa are revised.

Summary.

Australian workers have been interested for some time in the common *Ceroplastes* on coffee in Kenya as a source from which parasites of *Ceroplastes destructor* Newst. might be obtained.

The doubt that more than one white waxy scale occurs on coffee in East Africa led to an examination of material of *C. destructor* and certain other allied species. It was found that *C. destructor* was present in Uganda and Kenya but did not occur on coffee in Kenya, so far as is known at present. *C. brevicauda* Hall, here raised to specific rank, was found to occur on coffee in Uganda and a new species, *C. luteolus*, on the same crop in Kenya.

Descriptions of *C. luteolus*, *Lecaniodiaspis erratica* and *Pseudococcus latipes*, spp. n., all from coffee, are given.

Acknowledgements.

The writer wishes to thank Dr. R. H. Le Pelley, Senior Entomologist, Department of Agriculture, Kenya, for the help given in obtaining the large amount of material required for the study, for his interest in the work and for reading the manuscript; Dr. W. J. Hall, Director, Commonwealth Institute of Entomology, London, who presented typical material of *C. brevicauda* from Southern Rhodesia; and Prof. H. Morrison, U.S. Department of Agriculture, Washington D.C., who kindly examined and commented on the species of *Lecaniodiaspis*. Thanks are also due to Dr. F. Wilson, Commonwealth Scientific & Industrial Research Organisation, Canberra, as well as Mr. A. P. G. Michelmore, Senior Entomologist, Department of Agriculture, Uganda, for the valuable lots of material they forwarded from Australia and Uganda, respectively.

References.

GURNEY, W. B. (1936). Agric. Gaz. N.S.W., **47**, pp. 453–456, 464, 472.

HALL, W. J. (1931). Trans. R. ent. Soc. Lond., **79**, pp. 285–303.

HALL, W. J. (1945). Bull. ent. Res., **36**, pp. 305–313.

NEWSTEAD, R. (1910). Bull. ent. Res., **1**, pp. 185–199.

NEWSTEAD, R. (1917). Bull. ent. Res., **8**, pp. 1–34.

MOSQUITOS AND MALARIA IN THE HILL COUNTRY OF THE NEW HEBRIDES AND SOLOMON ISLANDS.[1]

By Marshall Laird.[2]

L.C.

Anopheles (*Myzomyia*) *punctulatus* Dön. and *A.* (*Myzomyia*) *farauti* Lav. are the mosquitos chiefly concerned in the transmission of malaria in Australasia (Lee & Woodhill, 1944). Both are common in the Solomon Islands, where certain additional species were discovered during the war in the Pacific (Belkin, Knight & Rozeboom, 1945), but *A. farauti* is the sole representative of its genus in the New Hebrides.

Few observations concerning the occurrence of the Pacific Anophelines in mountainous country have been published. The available information regarding the presence of *A. punctulatus* at relatively high altitudes is from New Guinea, Taylor (1934) reporting that this species is to be found there both on the coast and in inland districts up to 3,500 ft. above sea level. As regards *A. farauti*, Lee & Woodhill (1944) considered this insect (= *A. punctulatus* var. *moluccensis* Sw. & Sw.) to be characteristic of low-lying areas, stating that the only record of its occurrence at any considerable elevation was from 2,000 ft. on the Atherton Tableland (Queensland, Australia). However, *A. farauti* has since been recorded from altitudes of up to 5,800 ft. in New Guinea (Lee, 1946).

Lambert (1949) declared that "In Papua, a walk of a few miles inland from the beach brings one to a malaria-free belt in the mountains among practically untouched peoples" and referred to a personal communication from Dr. W. M. Strong who, after long experience of tropical medicine in Papua, was of the opinion that neither *Anopheles* nor malaria occurred far from the coast there. It was also pointed out by Lambert that the recruiting of Papuan hill people for plantation labour had had to be suspended, as these people quickly succumb to malaria when brought down to the coast.

The literature is of little assistance in connection with the presence or absence of *Anopheles* in the hill country of the New Hebrides and Solomon Islands. Marshall (1937) had gained the impression that the higher inland districts of Espiritu Santo, New Hebrides, were free from Anophelines and malaria. No new data from the interior of that island were forthcoming as a result of malariological activities during World War II, the considerable volume of work then undertaken being confined to the coastal areas (Daggy, 1945). Daggy did, however, report *A. farauti* from the interior of Gaua Island in the Banks Group, to the north of Espiritu Santo. During a week spent there, at Steaming Hill Lake (altitude, 1,100 ft.), he found this Anopheline to be abundant. It is of interest to observe that Baker (1929), who spent a week at Steaming Hill Lake in 1927, noted that "one of the most remarkable facts about the animals of the Lake is the absence (while we were there, at any rate) of biting mosquitoes." J. G. Miller (unpublished report, 1947), referring to inland Espiritu Santo, stated that "We saw no mosquitoes and the people say they do not get fever unless they go down to the coast."

In the Solomons, larvae of *Anopheles* (*Myzomyia*) *solomonis* Belkin, Knight & Rozeboom (the significance of which as a vector of *Plasmodium* is unknown) have been taken at elevations of up to 1,500 ft. (Belkin, Knight & Rozeboom, 1945—north-western Guadalcanal). There are no records of other Anophelines from higher altitudes in the Group. Neither are there any data concerning the occurrence of malaria in the interior of Guadalcanal or of other mountainous islands of the Solomons. Planters and other residents of long standing in both this Group and the New Hebrides tell the same story as that heard by Lambert in Papua—namely, that natives from the interior are very prone to succumb to bad bouts of malaria on coming out to the coast. It is generally believed that the mountainous interiors of the larger islands are malaria-free.

---

[1] These studies form part of a project initiated by the Royal New Zealand Air Force and supported by a grant from the N.Z. Department of Scientific and Industrial Research. Their publication is authorised by the Chief of Air Staff, RNZAF.

[2] Medical Branch, RNZAF. Now with Department of Parasitology, University of Malaya.

The data presented hereunder were collected in the course of brief visits to hill villages of Espiritu Santo and Guadalcanal, undertaken for the purpose of seeking first-hand information on the altitudinal range of *Anopheles* and malaria.

ESPIRITU SANTO, NEW HEBRIDES.

The original intention had been to follow the west coast route described by Baker (1929), who called at villages at altitudes of 3,500 ft. and 4,000 ft. on his ascent of Mount Tabwemasana. This plan had to be abandoned, owing to the impossibility of obtaining the necessary sea transport from Segond Channel (where European settlement is concentrated, at the south-east corner of the island) at the time of the visit.

Alternative arrangements thus having to be made, it was decided to go to a little-known upland district just south of Mount Laiiriiri (5,500 ft.) in the south-western part of the island. The trip was arranged by, and made in the company of, the British District Agent, Mr. D. Freegard.

Leaving the coast at Tasmaloun on the morning of 2nd September 1952, we made our way inland up the valley of the Nevaka river. Mosquito collections were made wherever possible. It being the dry season, though, Anopheline larval habitats were not plentiful. The first one encountered was in the vicinity of Biase village, something over a mile from the coast. Numerous larvae of *A. farauti* and *Aëdes* (*Aëdes*) *lineatus* (Taylor) were found there, in hoof-print pools in a swampy clearing.

The next collection was made four miles upstream, from a seepage pool in the bed of a dried-up tributary (altitude, 500 ft.). A few early instars of *Anopheles farauti* were the only mosquito larvae present. The valley of the Nevaka and the beds of some of its tributaries are traversed by hill people during journeys to the coast, but the nearest actual settlement to this larval habitat was three miles away. As the flight range of *A. farauti* is usually less than one mile and has not been known to exceed this distance (Daggy, 1945; Roberts & O'Sullivan, 1948; Perry, 1950) it is highly unlikely that adult mosquitos emerging from the pool could reach the village in question—especially in view of the presence of a barrier of jungle. Such mosquitos could thus have only infrequent opportunities of feeding upon human blood. The only warm-blooded vertebrates constantly accessible to them would be fruit bats, wild pigs and birds, as Daggy had previously found to be the case at Steaming Hill Lake, Gaua. Precipitin tests made in New Guinea and Queensland have shown that "wild" *A. farauti* adults feed from a wide range of hosts, including birds and various mammals, and probably merely attack whatever animal happens to be nearest at hand (Lee & Woodhill, 1944; Roberts & O'Sullivan, 1948).

As the valley of the Nevaka narrowed and the course of the river became steeper, no ground pools other than those formed in small rock crevices were to be found. Only Culicine larvae—*Culex* (*Mochthogenes*) *femineus* Edw.—were present in these. No further Anopheline larval habitats were located until the following morning, when a few *A. farauti* larvae were collected from a small seepage pool at an elevation of approximately 1,100 ft. This pool was near a lean-to shelter by a prawn trap which had been constructed across the stream. It was some 12 miles from the coast, the nearest village being about a mile away and at the top of a thickly forested spur which rose steeply out of the valley.

The village concerned, Namatasopa, occupies a clearing more than 2,000 ft. above sea level. It was reached later in the morning, and arrangements were made for the night to be spent there. Runners were sent to the nearby villages of Povo and Cheripai to bring in as many people as possible for a blood-smear survey. All three villages are typical of the hill country of Espiritu Santo in supporting only small populations, the number of inhabitants in each ranging from 15 to 30.

Meanwhile, three hours were spent in a search for mosquito breeding places in the vicinity of Namatasopa. The ground sloping away steeply on three sides, and a narrow ridge trending upwards at the rear, the whole site was so well drained that no surface water could lie there for more than brief periods. Temporary pools formed in the clearing during rainy weather could hardly persist long enough for mosquitos to become established in them. The only pool found near the village was a small one by the track-side some 300 yd. away. A thin trickle of water from a hillside spring had been dammed to form a washing place, which was rendered quite unsuitable as a larval habitat for *A. farauti* by the constant splashing of water into it from a bamboo spout above. Only three insects, water beetles of the genus *Platynectes*, were collected there.

Below this washing place the ground fell away too steeply to allow of pool formation. However, an area of waterlogged ground supported a number of taro plants (*Alocasia* sp.), and water held in the leaf axils of these contained several larvae of an undescribed *Tripteroides*.* No other mosquitos were encountered in the area. Particularly noteworthy was the complete absence of day-biting pest species. These, chiefly *Aë. lineatus* and *Aë.* (*Stegomyia*) *scutellaris* (Wlk.), had ceased to be troublesome when the wide lower reaches of the Nevaka were left behind.

Blood-smears were not taken from any adult villagers. Most of the men had been down to the coast from time to time, and the few women who were in evidence were too timid for preparations to be obtained. A total of 16 children from Namatasopa, Povo and Cheripai had been assembled by late afternoon. Both thick and thin blood-smears were taken from these, the results of subsequent microscopic examination of the preparations being set out in Table I.

All five children harbouring *Plasmodium vivax* had grossly enlarged spleens, although splenomegaly was not evident in the two positive for *P. malariae*. With but a single exception, none of the 16 children examined had ever been down to the coast. All of them, though, had frequently accompanied their parents on prawning trips along the Nevaka; and from time to time they had stayed overnight in temporary shelters in the valley.

No mosquito bites were suffered during the night spent in one of the three dwellings at Namatasopa. A careful search of the thatched walls and roofs of these dwellings was made soon after dawn on the following morning. No mosquitos were found, and we were assured by the villagers that these insects never bother them in the hills.

From the facts that *Anopheles farauti* was found breeding here and there along the Nevaka and its tributaries to the furthest inland point investigated, and that the vicinity of Namatasopa is both free from potential Anopheline larval habitats and inaccessible to Anophelines breeding elsewhere, it is concluded that the six infected children who had never visited the coast had contracted malaria during overnight visits to the prawning grounds in the valley, infected people returning from trips to the coast having initially acted as *Plasmodium* reservoirs for the valley *Anopheles*.

---

* Dr. J. N. Belkin of the University of California, who is at present dealing with the mosquito collections formed by American entomologists who served in the South Pacific during the war years, has examined these larvae. He informs me (private communication, 1954) that they belong to a species, also known from leaf axils of banana and sago palm, which he proposes to describe as new.

TABLE I.

Analysis of blood-smear examinations, Namatasopa district.

Age of children (years)	No. without parasites	No. with *P. falciparum*	No. with *P. vivax*	No. with *P. malariae*	Total No. children
Under 1	1	0	0	0	1
1 — 4	4	0	1	1	6
5 — 9	4	0	3	1	8
10 — 14	0	0	(1)	0	1
Total	9	0	4+ (1)	2	16

The bracketed number indicates the only child who had visited the coast.

GUADALCANAL, SOLOMON ISLANDS.

My wife and I made a field trip into the interior of Guadalcanal in the dry season of 1953. The route followed during this journey (August 3–9) is outlined in fig. 1. Mosquito collections were made throughout each day's march and at the villages, while blood-smears were taken during overnight stops at Betilonga, Tuturahitoko, Malakuna and Talamu. All of these hill villages are substantially larger than those dealt with on Espiritu Santo. Each held about 60 people at the time of our visit, but an accurate census could not be made in the time available because of the absence of many of the inhabitants on journeys of one kind or another. All altitudes were measured by altimeter.

Betilonga (1,750 ft.).

This village was reached after a seven-hour tramp along bush tracks from a point near the coast two miles east of Honiara, the centre of administration for the British Solomon Islands Protectorate and the seat of the Western Pacific High Commission.

Larvae of *Anopheles solomonis* were collected from small seepage pools along the Belaha river, where this stream flows past Betilonga. Four hours' collecting on two successive days yielded only five larvae, which were dipped from amongst dead leaves and emergent vegetation in pools all but concealed by waist-high grass. This is in accord with the experience of Belkin, Knight & Rozeboom (1945) who stated that "practically all the collections were made in deeply shaded areas in flotage of sticks or in leaves along the margins of the pools. The larvae are difficult to locate and are very scarce."

The only mosquitos found in association with *A. solomonis* in these pools were *Uranotaenia civinskii* Belkin and *Culex* (*Lophoceraomyia*) *fraudatrix* Theo. Larvae and pupae of *C.* (*Culex*) *squamosus* (Tayl.) were abundant in masses of

Spirogyra along the margins of the stream itself, but no Anophelines could be found there.

Blood-smears were taken from 21 of the villagers. Unfortunately, only three children below 15 years of age (*i.e.*, within the group most likely to harbour sufficient numbers of malaria parasites for demonstration by ordinary field techniques) were brought forward for examination. The remaining 18 were all adults, their ages ranging up to about 50 years. It should be pointed out that all the ages recorded herein, with the exception of those of very young children, are approximate only. " Bush " Solomon Islanders of more advanced years rarely have the slightest idea of how old they are, and age so rapidly that a man still in his forties is apt to be so grizzled and bowed as to pass for at least eighty.

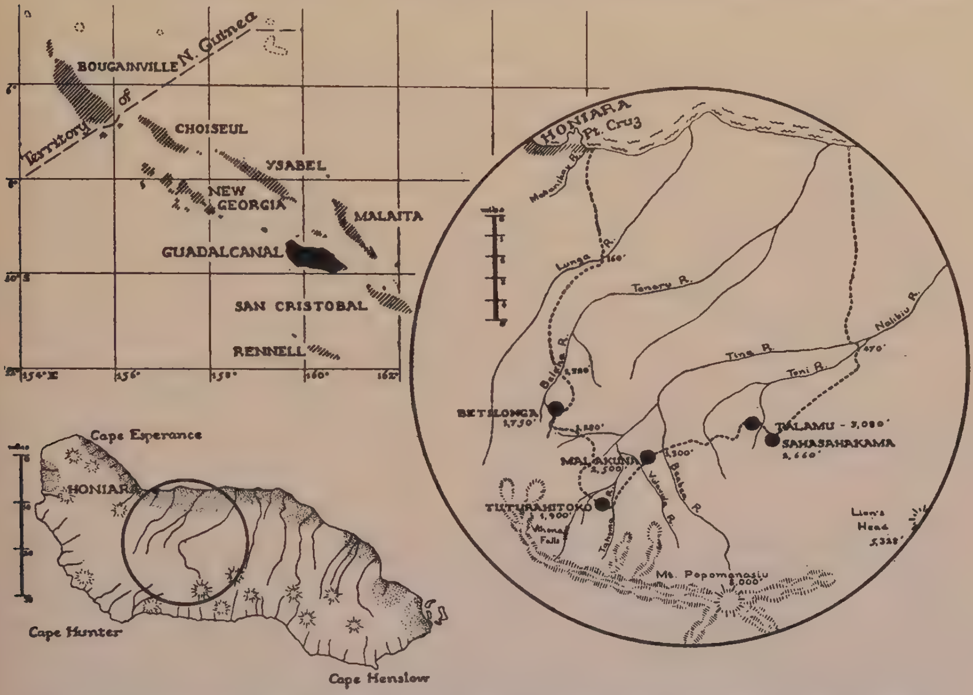

BOUGAINVILLE
Territory of N. Guinea
CHOISEUL
YSABEL
NEW GEORGIA
MALAITA
GUADALCANAL
SAN CRISTOBAL
RENNELL
154° E
156°
158°
160°
162°
10° S
Cape Esperance
HONIARA
Cape Hunter
Cape Henslow
HONIARA
Pt. Cruz
Matanikau R.
Lunga R.
Tenaru R.
Balehe R.
Tina R.
Toni R.
Nalibiu R.
BETILONGA 1,750'
MALAKUNA 2,500'
TUTURAHITOKO 1,900'
TALAMU - 3,080'
SAHASAHAKAMA 2,660'
Vhonai Falls
Tahamo R.
Valevula R.
Balehe R.
Lion's Head 5,328'
Mt. Popomanasiu 8,000'
miles

Fig. 1.—Illustrating the location of the area of Guadalcanal traversed. Detail within the enlarged circle is largely from Pastor Clark's sketch map, the remainder after official sources.

All preparations were made from 2200 hr. onwards, so that nocturnally periodic microfilariae would be noted as well as malaria parasites. Although several of the older people claimed to have suffered from " fever " from time to time, no haematozoa whatsoever were recorded. This, at least insofar as *Plasmodium* is concerned, is probably partly attributable to the difficulty of demonstrating malaria parasites in the blood of adult Melanesians not actually suffering from an attack of the disease at the time of preparation of the smears.

Tuturahitoko (1,900 ft.).

The journey to this village along the rugged track from Betilonga was made on 5th August. With several halts for collecting, it occupied eight and a half hours. Tuturahitoko, like the previous village, is built on relatively flat ground immediately above a river. It lies close beneath the main mountain backbone of the island, and is about 16 miles from the north coast and 10 from the south coast.

Three species of mosquitos were recorded by the track-side on the way from Betilonga:—*Tripteroides* (*Rachisoura*) *mathesoni* Belkin, *Uranotaenia quadrimaculata* Edw. and *Aëdes* (*Finlaya*) *papuensis* (Tayl.). Larvae of the first two species were common in the leaf axils of taro (*Alocasia* sp. and *Colocasia antiquorum* var. *esculenta*), although as *T. mathesoni* is highly predacious and cannibalistic (Belkin, 1950) an axil containing a well-developed larva of this species seldom supported more than a very few other larvae of either mosquito. Numerous larvae of *U. quadrimaculata* were collected from water in the bases of fallen palm fronds on the summit of a hill at an elevation of 2,600 ft. The developmental stages of *Aë. papuensis* were often abundant in small pools in pot holes and creviced boulders in the beds of rocky streams.

Many larvae of *Anopheles punctulatus* were recorded from the immediate vicinity of Tuturahitoko. Some were found in a small track-side pool filled with muddy water and fully exposed to sunlight, while the remainder were taken from a clear, unshaded seepage pool alongside the Tahoma river by the village washing place. No mosquito larvae of other species were present in either habitat.

Blood-smears were taken from 25 villagers. Five of them were below 15 years of age, the others ranging up to 40 or 50. Only four of those seen, children of from four to seven years of age, had never been out to the coastal plains. One of these was parasitised by *P. vivax,* while a man of 20 years of age proved to harbour *P. malariae.* This man had recently visited the coast, but the child's infection could only have been acquired locally. Although the films were again prepared at night-time, this time from 2100 hr. onwards, *Wuchereria* was not recorded.

Malakuna (2,500 ft.).

Aë. papuensis was again plentiful in the stream beds crossed during the two-hour tramp from Tuturahitoko. Malakuna is a typical Solomon hill-top village, occupying a narrow strip of cleared land along the summit of a steep-sided ridge. No potential Anopheline breeding places were present there, the nearest being in the gorges of the Vulavula and Beabea rivers to either side of the ridge and respectively 860 ft. and 1,200 ft. below it. Larvae of *T. mathesoni* and *U. quadrimaculata* were common in taro axils about the village. On one occasion a single larva closely comparable with that of *Culex* (*Acallyntrum*) *perkinsi* Stone & Penn was associated with *U. quadrimaculata* in one of these axils (see systematic appendix).

Twenty-eight of the villagers were examined for haematozoa at 2100 hr. Once again no microfilariae were demonstrated, but 7 (25%) of those seen were positive for *Plasmodium* (Table II).

Only three of those examined, all children of nine years of age or less, had never been out to the coastal plains. One of these harboured *P. vivax* and another *P. malariae*, infections which could not have been contracted at Malakuna other than in the most unlikely event of Anophelines having reached there from the deep valleys on either side (and through thick forest at that). However, all the people of Malakuna pay frequent visits to Tuturahitoko. As *A. punctulatus*, a proven vector of *P. vivax* and *P. malariae* (see Mackerras & Roberts, 1947; Mackerras & Ercole, 1948), occurs there in the presence of a reservoir of infection of these parasites, transmission could easily have taken place at that village. All three adults infected were complaining of " fever ", and had but recently returned from a visit to the coast.

Talamu (3,080 ft.).

This village, the highest visited and probably among the highest in the Protectorate, is a little over four hours' march from Malakuna and somewhat closer to the north coast. *T. mathesoni*, *U. quadrimaculata* and *Aë. papuensis* were collected from all suitable larval habitats encountered during the journey. The only other Culicine encountered was an undescribed species of *Corethrella*, two larvae of which were siphoned from water held in a leaf axil of *Pandanus* at an altitude of 3,000 ft. *T. mathesoni* and *U. quadrimaculata* larvae occurred plentifully in leaf axils of *Colocasia antiquorum* at the village itself.

TABLE II.

Analysis of blood-smear examinations, Malakuna.

Age of persons (years)	No. without parasites	No. with *P. falciparum*	No. with *P. vivax*	No. with *P. malariae*	Total No. persons
Under 1	0	0	0	0	0
1 — 4	0	0	0	1	1
5 — 9	1+(2)	0	1	(1)	5
10 — 14	(1)	0	0	(1)	2
15 — 19	(1)	0	0	0	1
20 — 24	(2)	0	(2)	0	4
25 — 29	(5)	0	(1)	0	6
30 plus	(9)	0	0	0	9
Total	1+(20)	0	1+(3)	1+(2)	28

The bracketed numbers indicate those who had at some time visited the coast.

Two larvae of *Anopheles solomonis* were dipped from a dammed-up mountain stream, used as a washing place, about half a mile from Talamu and at an elevation of 3,000 ft. The places utilised as larval habitats by this mosquito are very similar to those in which the aquatic stages of *A.* (*Myzomyia*) *lungae* Belkin & Schlosser occur at lower altitudes in north-western Guadalcanal, and also resemble the breeding places of *A.* (*Myzomyia*) *superpictus* Grassi at comparable altitudes in Macedonia (Wenyon, 1921). All three species favour small pools in the beds of streams subject to frequent flooding, and all three display a larval behaviour-pattern indicating a resistance to the periodic flushing-out of their breeding places. Thus larvae of both Guadalcanal species readily wriggle out of the water on to the bank or objects floating in the water (Belkin, Knight & Rozeboom, 1945), while those of *A. superpictus* are " even found on the damp, sandy margin of the stream and not actually in water " (Wenyon, 1921).

Microfilariae were not recorded from any of the 26 villagers from whom blood-smears were taken (at 2100 hr.), but 6 (23%) of these harboured *Plasmodium* (Table III).

As Table III indicates, only five of those examined at Talamu, all children of up to four years of age, had never been down to the coast; and three of the five were positive for *P. malariae*. One of these was a six-month-old child, whose father insisted that it had never been taken down into the deep valleys below Talamu—which, like Malakuna, is built on a lofty and steep-sided ridge.

If this child had not, indeed, ever been away from its village, the manner in which transmission took place poses something of a problem. There was no surface water, and no indication that there ever would be potential breeding places for any of the Guadalcanal Anophelines, at Talamu itself. No mosquitos of any kind were troublesome either there or at any other hill-top village during this reconnaissance. It should be mentioned, though, that Dr. A. J. Cain and Mr. I. C. J. Galbraith of Oxford University, who were studying the ornithology of the interior of Guadalcanal at the time of this visit, assured me that they had been bitten by *Anopheles* while spending a night under canvas on a ridge inland from Betilonga and 4,000 ft. above sea level.

TABLE III.

Analysis of blood-smear examinations, Talamu.

Age of persons (years)	No. without parasites	No. with *P. falciparum*	No. with *P. vivax*	No. with *P. malariae*	Total No. persons
Under 1	0	0	0	1	1
1 — 4	2+(1)	0	0	2	5
5 — 9	(1)	0	(1)	(1)	3
10 — 14	0	0	0	0	0
15 — 19	0	0	0	0	0
20 — 24	(4)	0	0	(1)	5
25 plus	(12)	0	0	0	12
Total	2+(18)	0	(1)	3+(2)	26

The bracketed numbers indicate those who had at some time visited the coast.

The larval habitat of *A. solomonis* located near Talamu, being completely surrounded and overhung by thick vegetation and full of dead leaves and other flotage, was quite unsuited to the requirements of *A. punctulatus*. It seems highly unlikely that the latter species, the only known malaria vector yet recorded from the interior of Guadalcanal, could become established anywhere in the vicinity of hill-top villages. However, unless prenatal infection took place, at least one primary case of quartan malaria seems to have been contracted at Talamu. In view of this, and of the experience of Cain and Galbraith, an investigation into the habits of *A. solomonis* and the ability of this species to transmit the malarial organisms would be of value.

One further village was passed through on the way back to the lowlands. This was Sahasahakama, under two hours' march from Talamu and on a neighbouring ridge at an altitude of 2,660 ft. Larvae of *Aë. papuensis* were collected from rock crevices at the edge of a swiftly-flowing stream between the two villages. There was no surface water in the vicinity of Sahasahakama, the houses being built on shelving and well-drained ground. Very few people were in evidence, and we were given to understand that most of the villagers were clearing ground for a new garden in the valley of the Toni river.

The route into this valley followed a long ridge trending towards the coast. After an initial climb to a little over 3,000 ft., some larvae of *U. quadrimaculata* being found on the way in water cupped in the base of a fallen palm frond, the track led downhill for four hours. The only water located during this period was in a small hole in the ground among the roots of a fallen tree, at an altitude of 2,080 ft. This water was full of dead leaves, very turbid and reddish in colour. The presence of a few dragonfly larvae indicated that the pool had probably persisted for some time. All stages of *Culex* (*Culiciomyia*) *papuensis* (Tayl.) were collected there (see systematic appendix).

On reaching the Toni river at an altitude of some 500 ft. above sea level, the following five mosquitos were found breeding in ox-bow pools:—*A. punctulatus*, *Culex* (*Lutzia*) *halifaxii* Theo., *C.* (*Culiciomyia*) *pullus* Theo., *C.* (*Culex*) *annulirostris* Skuse and (in marginal aggregations of *Spirogyra*) *C. squamosus*. All these species are common on the coastal plains, the first and last being the only ones collected in the hill country.

When the new Sahasahakama gardens were reached, it was found that tree-felling activities and the practice of throwing lopped-off branches into the river had created numerous marginal pools and still backwaters fully exposed to sunlight and ideally suited to the requirements of *A. punctulatus*. An average of 60 larvae of this species were collected there with each dip of a 200 cc. ladle.

All the members of the three Sahasahakama families in residence claimed to be suffering from " fever ", and several requests were made for quinine. Unfortunately, all the microscopic slides brought had by that time been used in the interior on both human and animal subjects. It was thus not possible to ascertain the relative species-incidence of *Plasmodium*. Adult *A. punctulatus* were abundant from early evening onwards. Altogether, the conditions called to mind those under which explosive population-increases of this species took place from time to time during the Pacific war (Laird, 1946).

A range of low hills still had to be crossed before reaching the inland margin of the coastal plains after a further two-hour journey. The circumstances attending the establishment of these gardens certainly illustrate how Guadalcanal hill people may become subject to severe malaria without actually going out to the coast at all.

Conclusions.

Only one Anopheline, *Anopheles farauti*, occurs in the New Hebrides. This species extends up the valley of the Nevaka river in south-western Espiritu Santo, and presumably is to be found along other such rivers until their valleys become narrow gorges not offering favourable larval habitats. There are not, however, any suitable larval habitats for *A. farauti* in the vicinity of such a hill-top village as Namatasopa. The steepness of the adjacent slopes is such that the only surface water present is that in the heavily-shaded beds of mountain torrents. Although these may become ponded in long dry periods, and the hill people dam some of them to form washing places, there is no evidence to show that *A. farauti* occurs in the upper reaches. It is considered that the demonstration of *Plasmodium vivax* and *P. malariae* in the blood of children who had never visited the coast is explained by these making periodic prawning trips to valley habitats of *A. farauti* in the company of malarial adults. The latter are especially subject to relapses during such trips, in consequence of the marked temperature changes accompanying the change in altitude. It should be mentioned in this connection that one of the coastal " boys " taken to Namatasopa as a bearer suffered a severe relapse of benign tertian malaria during the journey. In this instance, the unwontedly strenuous nature of his activities in carrying a pack through rough country was probably a contributory cause of the relapse.

The fact of the occurrence of *A. punctulatus* at altitudes of at least 1,900 ft. in the very heart of Guadalcanal sufficiently accounts for the local transmission of *P. vivax* and *P. malariae* in the vicinity of such valley villages as Tuturahitoko.

Like those of the New Hebrides, Guadalcanal hill-top villages do not afford suitable larval habitats for Pacific Anophelines. Although *A. solomonis* has now been collected from a mountain stream at an elevation of 3,000 ft., the significance of this species as a vector of *Plasmodium* remains unknown. In all but one of the cases which came to notice—that of the child which had never been away from Talamu, which leaves room to postulate that *A. solomonis* might be implicated—Guadalcanal hill children harbouring malaria parasites could have become infected during visits to valley villages if not to lowland cultivations such as those of the Sahasahakama people.

The non-discovery of *P. falciparum* and of *Wuchereria* in a total of 100 hill people of all ages examined on Guadalcanal is of decided interest. American studies of coastal natives from this island during World War II indicated that the former parasite is found in all age groups and takes second place to *P. vivax* among those of six years of age and over (Levine & Harper, 1947). These two authors also noted a 22 per cent. microfilaria rate for *W. bancrofti* in the lowlands of Guadalcanal. The dry season is admittedly hardly the best time for searching for *P. falciparum*, which tends to be associated with wet-season epidemics in the Solomons (Lambert, 1949). Nevertheless, although some future survey during December–May might reveal that the transmission of this parasite does indeed take place in the interior, it is to be remembered that the hill country of Guadalcanal receives much more rain throughout the year than does the coast. Marked fluctuations in the populations of vector Anophelines thus might not occur in the hills. Finally, the non-discovery of microfilariae could well be correlated with the apparent absence of *A. farauti*, the principal intermediate host of *W. bancrofti* in the Solomons (Byrd, 1946), from the more elevated parts of Guadalcanal.

Summary.

Anopheles (*Myzomyia*) *farauti* Lav. is recorded from the upper reaches of the Nevaka river, south-western Espiritu Santo, New Hebrides, to an altitude of 1,100 ft. and a distance of 12 miles from the coast. The presence of *Plasmodium vivax* and *P. malariae* in the blood of children from hill villages with no nearby Anopheline larval habitats is noted. These children, most of whom have never visited the coast, become exposed to infection during prawning trips to the valleys below their homes. The transmission of *P. vivax* and *P. malariae* is shown to take place in the interior of Guadalcanal, British Solomon Islands Protectorate, where a proven vector, *A.* (*Myzomyia*) *punctulatus* Dön., breeds at altitudes of up to at least 1,900 ft. above sea level. *A.* (*Myzomyia*) *solomonis* Belkin, Knight & Rozeboom, the status of which as a vector of *Plasmodium* is unknown, was found breeding at an altitude of 3,000 ft. Neither *P. falciparum* nor *Wuchereria bancrofti* were recorded from the hill districts visited. During the investigations several species of Culicines were collected. Features of the larval morphology of some of these are illustrated and briefly discussed in a systematic appendix.

Acknowledgements.

The authorities of the Western Pacific High Commission and the High Commission for France in the New Hebrides willingly co-operated in permitting these studies to take place in territories under their jurisdiction. All major transportation was by flying boats of No. 5 Squadron, RNZAF.

I am grateful to my wife for her invaluable help as my field assistant; to Mr. D. Freegard for his ready assistance on Espiritu Santo; and to Pastor Clark of the South Seas Evangelical Mission, for the loan of his excellent sketch map of the interior of Guadalcanal. Dr. J. N. Belkin kindly checked my identifications of some of the lesser-known CULICIDAE.

SYSTEMATIC APPENDIX.

All the New Hebridean Culicines referred to, with the exception of the new species of *Tripteroides*, have larval characters as figured by Lee (1944). As this new species is being described elsewhere by Belkin, it will not be mentioned further here.

The Anopheline larvae are as described and figured by Belkin, Knight & Rozeboom (1945). In both *Anopheles punctulatus* and *A. solomonis* the tubercles of prothoracic hairs 1 and 2 are always more or less widely separated from one another. These tubercles are small and unpigmented in the former species, and the shafts of the hairs themselves are quite slender (fig. 2, a). *A. solomonis* larvae, on the other hand, have prothoracic hairs 1 and 2, and the basal tubercles of these hairs, large and heavily pigmented (fig. 2, b). The larvae of *A. solomonis* are easily distinguished from those of the closely related *A.* (*Myzomyia*) *lungae* in that hair 1 of abdominal segment II, which has slender and unnotched leaflets in the latter species, is a large palmate structure having broad, notched leaflets (fig. 2, c) in the former.

Immature stages of *Tripteroides mathesoni* and *Uranotaenia civinskii* answer well to the detailed descriptions published by Belkin (1950, 1953); while the larvae of *Aëdes papuensis*, *Culex fraudatrix*, *C. halifaxii*, *C. pullus*, *C. squamosus* and *C. annulirostris* are as described and figured by Lee (1944).

It is considered that the larva exhibiting a striking constriction of the anal gills (fig. 2, d, e) is referable to *C.* (*Acallyntrum*) *perkinsi*. This species was described from the Tenaru area and the Umasini river in north-western Guadalcanal (altitude not stated, the records presumably being coastal ones). With the exception of a single record from a tree hole, the developmental stages of this species have previously been found only in leaf axils of *Pandanus* (Stone & Penn, 1948). The collection of a *C. perkinsi* larva from a leaf axil of *Colocasia* is thus of some interest.

King & Hoogstraal (1946) indicated that the larva of *Culex* (*Culiciomyia*) *papuensis* was confused with that of *C. pallidothorax* Theo. by Lee (1944), Lee's illustration of *C. papuensis* really being referable to *C. fragilis* Ludl. Adults reared from my Guadalcanal larvae lack the pale abdominal bands characteristic of *C. pallidothorax*, but the larvae themselves are undoubtedly very close indeed to those of the latter species as figured by Lee (after Senior White) and by Bohart & Ingram (1946). One feature of difference is that the two-branched fifth pentad hair, which is plumose in my specimens and is so figured by King & Hoogstraal, is non-plumose in the Oriental *C. pallidothorax* according to the illustrations published by Lee and Bohart & Ingram. *C. papuensis* was collected in the Solomons by entomologists of the United States armed forces (Belkin, private communication, 1954). The terminal segments of a larva from Guadalcanal are illustrated (fig. 2, f) to show the distinctive, tapering siphon which cannot be confused with that of any other mosquito known from the Solomons.

The immature stages of *Uranotaenia quadrimaculata* are, as Belkin (1953) pointed out, extremely variable. Several of the larvae collected near Sahasahakama exhibit basal fusing of two (fig. 3, d) or three (fig. 3, b, c) of the sharply-pointed lateral comb scales. In one instance, two closely approximated fused pairs appear at first sight as four scales joined basally (fig. 3, a).

Lee (1944) gave the number of scales in the lateral comb of *U. quadrimaculata* as 4–6, while Belkin (1953) illustrated a larva having five such scales and gave the number for a fourth-instar larval exuvia, which he described in detail, as 6–6. The average for my material is six, the number of lateral comb scales for 10 successive normal fourth-instar larvae being 6–7, 6–6, 5–6, 6–7, 5–5, 6–7, 6–6, 6–5, 6–6 and 6–7. Ten fourth instars from the abnormal brood under discussion exhibited the following combinations:—(2) + 5 and (2) + 3; (2) + 3 and (2) + 4; 5 and 6; (2) + 4 and 6; 5 and (2) + 5; (2) + 4 and (2) + 5;

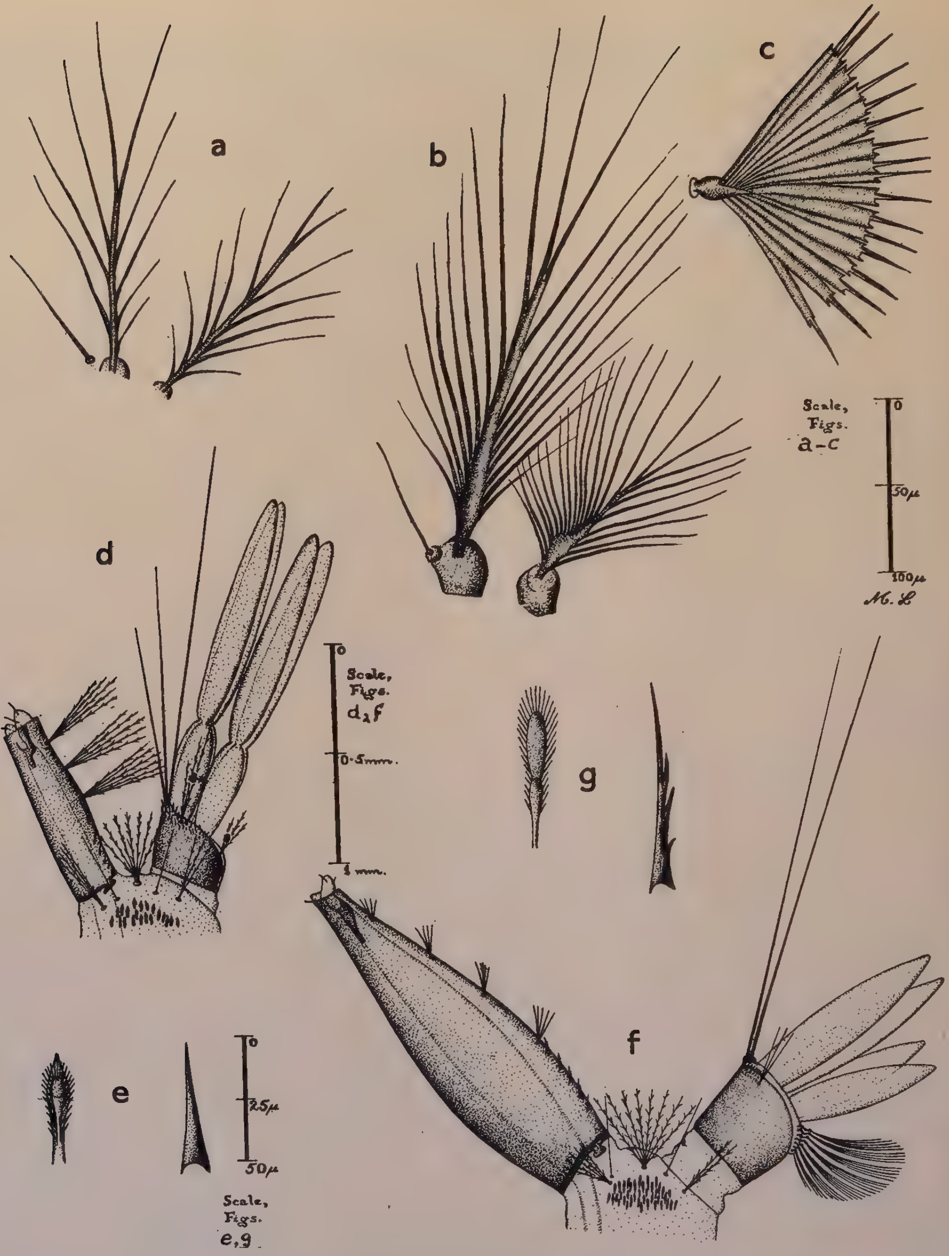

a
b
c
Scale, Figs. a-c
0
50μ
100μ
M. L.
d
0
Scale, Figs. d, f
0·5mm.
1 mm.
g
e
0
25μ
50μ
Scale, Figs. e, g
f

Fig. 2.—(a) *Anopheles (Myzomyia) punctulatus.* Shoulder hairs.
(b) *Anopheles (Myzomyia) solomonis.* Shoulder hairs.
(c) *Anopheles (Myzomyia) solomonis.* Hair 1, abdominal segment II.
(d) *Culex (Acallyntrum) perkinsi.* Terminal segments, lateral view.
(e) *Culex (Acallyntrum) perkinsi.* Lateral comb scale and pecten tooth.
(f) *Culex (Culiciomyia) papuensis.* Terminal segments, lateral view.
(g) *Culex (Culiciomyia) papuensis.* Lateral comb scale and pecten tooth.
(All figures prepared with the aid of a Zeiss-Winkel drawing apparatus, from alcohol-preserved specimens mounted in Canada balsam.)

(2) + 4 and 5; (3) + 3 and (2) + 3; (3) + 3 and (2) + 4; (2) + 5 and (2) + (2) + 3. The average number of lateral comb scales among these abnormal larvae remaining unchanged, this is clearly not a case of larval structures being duplicated (although Belkin has noted the common occurrence of larval hair duplication in this species). Penn (1947) described a similar basal fusion of lateral comb teeth in several batches of fourth-instar larvae of *Aë. scutellaris* from New Guinea. He regarded the phenomenon as indicative of " a primitive lateral plate of the type found in some species of the genus *Uranotaenia* ". In the instance under consideration, though, the species concerned, besides being a *Uranotaenia*, is actually one in which the comb plates are very well developed, being strongly sclerotised and united dorsally.

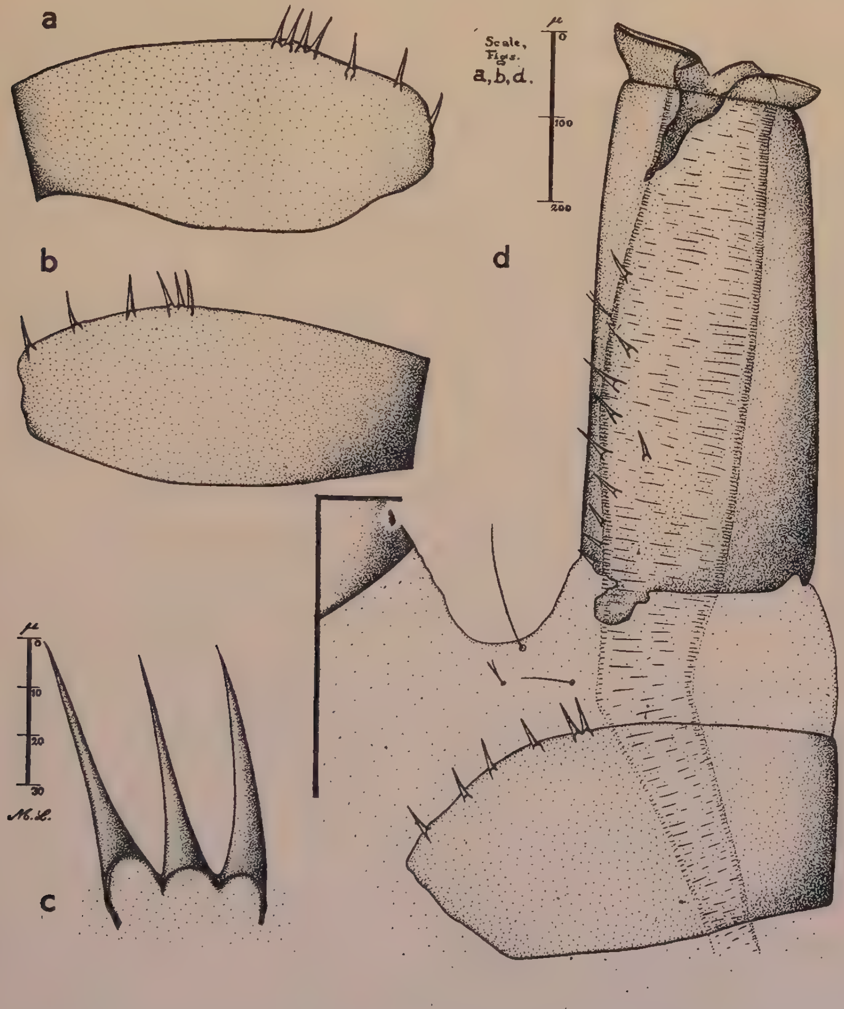


Fig. 3.—*Uranotaenia quadrimaculata.* (a) and (b) lateral comb plate, illustrating basal fusion of comb scales; (c) three lateral comb scales fused basally; (d) terminal segments, lateral view.

The number of pecten teeth occurring in larvae of *U. quadrimaculata* varies from four to seven according to Lee (1944), Belkin (1953) giving it as 6–7 in the larvae which he described fully. In my material the average is six, the number present in ten successive normal larvae being 6–7, 6–7, 6–6, 5–6, 6–7, 6–6, 5–6, 6–7, 6–6 and 5–6. Ten successive larvae from the abnormal brood, however, exhibited the following combinations:— 5–7, 7–7, 10–8, 7–8, 7–8, 7–8, 7–8, 8–8, 8–6, 7–8 (av., 7·5). No basally fused pecten teeth were noticed, but the average number of teeth in the pecten of those larvae having fused lateral comb teeth was thus significantly higher than normal. One larva had 10 irregularly-arranged pecten teeth on one side of the siphon (fig. 3, d) and 8 on the other. As Belkin has already suggested, the proneness of *U. quadrimaculata* larvae to various abnormalities would seem to render the species an excellent subject for the study of genetical variation.

Finally, both the *Corethrella* larvae collected near Talamu were early instars. They are probably referable to the species as yet undescribed, that was collected from sago-palm leaf axils (at 500 ft. to 1,000 ft.) on Guadalcanal during the war years (Belkin, unpublished report, 1945).

A check collection of the material discussed herein has been deposited at the Dominion Museum, Wellington, New Zealand. Specimens of *Tripteroides mathesoni*, the undescribed species of *Tripteroides*, *Uranotaenia civinskii*, *U. quadrimaculata*, *Aëdes papuensis* and *Culex papuensis* have been forwarded to Dr. J. N. Belkin for study and for ultimate deposition in the United States National Museum collections.

References.

Baker, J. R. (1929). Man and animals in the New Hebrides.—200 pp. London, Routledge.

Belkin, J. N. (1950). Mosquitoes of the genus *Tripteroides* in the Solomon Islands.—Proc. U.S. nat. Mus., **100,** pp. 201–274.

Belkin, J. N. (1953). Mosquitoes of the genus *Uranotaenia* in the Solomon Islands (Diptera: Culicidae).—Pacif. Sci., **7,** pp. 312–391.

Belkin, J. N., Knight, K. L. & Rozeboom, L. E. (1945). Anopheline mosquitoes of the Solomon Islands and New Hebrides.—J. Parasit., **31,** pp. 241–265.

Bohart, R. M. & Ingram, R. L. (1946). Mosquitoes of Okinawa and islands in the central Pacific.—NAVMED, no. 1055, 110 pp. Washington, D.C., Bur. Med. Surg., Navy Dep.

Byrd, E. E. (1946). Epidemiological investigations on filariasis on certain islands of the South Pacific area.—J. Parasit., **31,** suppl., p. 13.

Daggy, R. H. (1945). The biology and seasonal cycle of *Anopheles farauti* on Espiritu Santo, New Hebrides.—Ann. ent. Soc. Amer., **38,** pp. 1–13.

King, W. V. & Hoogstraal, H. (1946). The New Guinea species of *Culex* (*Culiciomyia*), with descriptions of two new species.—Proc. biol. Soc. Wash., **59,** pp. 143–153.

Laird, M. (1946). Observations on *Anopheles punctulatus* Dönitz, 1901, and *Anopheles farauti* Laveran, 1902, at Palmalmal and Manginuna, New Britain, during July and August, 1945.—Trans. roy. Soc. N.Z., **76,** pp. 148–157.

Lambert, S. M. (1949). Malaria incidence in Australia and the South Pacific.—*In* Boyd, M. F. *Ed.* Malariology, **2,** pp. 820–830. Philadelphia, Pa., Saunders.

LEE, D. J. (1944). An atlas of the mosquito larvae of the Australasian region.—(Issued by the Australian Military Forces.)

LEE, D. J. (1946). Records of *Anopheles* (Diptera, Culicidae) from high altitudes in New Guinea.—Aust. J. Sci., **8**, p. 165. (Original not seen: reference from Roberts, F. H. S. (1948). The distribution and seasonal prevalence of anopheline mosquitoes in north Queensland.—Proc. roy. Soc. Qd **59**, pp. 93–100.)

LEE, D. J. & WOODHILL, A. R. (1944). The anopheline mosquitoes of the Australasian region.—Monogr. Dep. Zool. Univ. Sydney, no. 2, 209 pp.

LEVINE, N. D. & HARPER, P. A. (1947). Parasitological observations on malaria in natives and troops, and on filariasis in natives.—Amer. J. trop. Med., **27**, no. 3, suppl., pp. 119–128.

MACKERRAS, M. J. & ERCOLE, Q. N. (1948). Observations on the life-cycle of *Plasmodium malariae*.—Aust. J. exp. Biol. med. Sci., **26**, pp. 515–519.

MACKERRAS, M. J. & ROBERTS, F. H. S. (1947). Experimental malarial infections in Australasian anophelines.—Ann. trop. Med. Parasit., **41**, pp. 329–356.

MARSHALL, A. J. (1937). The black musketeers: the work and adventures of a scientist on a South Sea island at war and in peace.—329 pp. London, Heinemann.

PENN, G. H. (1947). The larval development and ecology of *Aedes* (*Stegomyia*) *scutellaris* (Walker, 1859) in New Guinea.—J. Parasit., **33**, pp. 43–50.

PERRY, W. J. (1950). Principal larval and adult habitats of *Anopheles farauti* Lav. in the British Solomon Islands.—Mosq. News, **10**, pp. 117–126.

ROBERTS, F. H. S. & O'SULLIVAN, P. J. (1948). Studies on the behaviour of adult Australasian anophelines.—Bull. ent. Res., **39**, pp. 159–178.

STONE, A. & PENN, G. H. (1948). A new subgenus and two new species of the genus *Culex* L. (Diptera, Culicidae).—Proc. ent. Soc. Wash., **50**, pp. 109–120.

TAYLOR, F. H. (1934). The Diptera of the Territory of New Guinea. I. Family Culicidae.—Proc. Linn. Soc. N.S.W., **59**, pp. 229–236.

WENYON, C. M. (1921). The incidence and aetiology of malaria in Macedonia.—J. R. Army med. Cps, **37**, pp. 83–108, 172–192, 264–277, 352–365.

NOTES ON THE MOSQUITOS OF THE GILBERT, ELLICE AND TOKELAU ISLANDS, AND ON FILARIASIS IN THE LATTER GROUP.[1]

By Marshall Laird.[2]

There are 25 islands, many of them atolls composed of a number of islets, in the Gilbert and Ellice Islands Colony—a Crown Colony under the administrative control of the High Commissioner for the Western Pacific. These islands lie between the parallels of 03°15′N. and 10°45′S. and the meridians of 172°30′E. and 179°52′E. The 16 northernmost ones, the Gilberts, form an arc across the Equator. They are, in effect, a bridge between Polynesia and Micronesia, the affinities of the Gilbertese themselves being largely Micronesian. The people of the nine southern islands, the Ellice Group, are Polynesians.

New Zealand administers the Tokelau Group, which is made up of three atolls inhabited by Polynesians. Lying out to the east of the Ellice Islands, these atolls are bounded by the latitudes of 08°30′S. and 09°28′S. and the longitudes of 171°12′W. and 172°32′W.

Filariasis occurs throughout the area in question, being of the non-periodic type in the Polynesian islands. There is a certain amount of evidence to suggest that in the Gilberts the nocturnally periodic type is present as well (Backhouse & Heydon, 1950). Elephantiasis is particularly prevalent in the northern Ellice Islands (O'Connor, 1923), but is rare elsewhere.

Only one species of mosquito, *Aëdes* (*Stegomyia*) *pseudoscutellaris* (Theo.), has been reported from the Tokelau Group (O'Connor, 1923). O'Connor also found this mosquito to be widespread in the Ellice Islands, and demonstrated it to be the vector of *Wuchereria* both there and in the Tokelau Group. Buxton recorded "*Aëdes variegatus* var. *pseudoscutellaris*" from all the islands of the Tokelau Group and from all those of the Ellice Group with the exception of Nurakita, which he did not visit; he thus felt, considering both the wide distribution and the limited flight-range of the species, that it was not a recent introduction (Buxton & Hopkins, 1927). Stating that "the eggs of this insect are resistant to drying, and that they are sometimes laid in canoes" Buxton thought it likely that Polynesians sailing up from Samoa had been responsible for the initial introduction, and that subsequent inter-island canoe voyagers had broadcast *pseudoscutellaris* within the two Groups. Davis (1949) suggested that the aquatic stages of this mosquito could have been carried in the drinking-water containers with which the former ocean-going canoes were equipped. It is worth noting that such hollowed-out wooden containers are still manufactured—although mostly for the tourist trade—by Ellice and Tokelau natives.

Young (1927) reported the prevalence of "*Stegomyia pseudoscutellaris*" in the Gilbert and Ellice Islands Colony. His record seems to have been intended to apply specifically to the Gilberts, as he had at that time visited all the Gilbert Islands although he had not been to the Ellice Group. Bohart & Ingram (1946) indicated that the representative of the *scutellaris* group occurring in the Gilberts is *Aëdes* (*Stegomyia*) *marshallensis* Stone & Bohart, 1944, basing this conclusion on material from the atolls of Tarawa and Abemama.

---

[1] These studies form part of a project initiated by the Royal New Zealand Air Force and supported by a grant from the N.Z. Department of Scientific and Industrial Research. Their publication is authorised by the Chief of Air Staff, RNZAF.

[2] Medical Branch, RNZAF. Now at Department of Parasitology, University of Malaya.

It was demonstrated by Marks (1951) that Theobald's *Aëdes pseudoscutellaris* is actually confined to Fiji. She described the widely distributed vector of *Wuchereria* in Polynesia as a new species, *A.* (*Stegomyia*) *polynesiensis*. However, having no material from the Ellice and Tokelau Islands, she was unable to state definitely that the representative of the *scutellaris* group found there is in fact *A. polynesiensis*.

O'Connor (1923) found only one other species of mosquito in the Ellice Group. This, which he referred to as "*Culex jepsoni*", was subsequently recognised as *C.* (*Culex*) *annulirostris* Skuse by Edwards (1924). Although O'Connor reported this species from five of the Ellice Islands, Buxton found it at Funafuti only. The latter author was of the opinion that drought was the probable cause of his not securing *C. annulirostris* on other islands of the Group (Buxton & Hopkins, 1927).

Culex (*Culex*) *pipiens fatigans* Wied. was collected by the District Officer, Tarawa, in 1925 (Buxton & Hopkins, 1927). These authors also identified examples of *Aëdes* (*Stegomyia*) *aegypti* (L.) from Tarawa. Both domestic species were listed from the Gilberts by Young (1927) and in subsequent Annual Medical and Sanitary Reports of the Colony. Buxton & Hopkins considered that at the time of their researches both *C. p. fatigans* and *A. aegypti* were still absent from all the islands of the Ellice and Tokelau Groups. Twenty years later, however, the latter species had become established at Nanumea, the most northerly atoll of the Ellice Islands (Venner, 1944). Brygoo (1953) indicated the occurrence of *C. p. fatigans* as well as *A. aegypti* in the Ellice Group (his Tables "A" and "C"), but quoted no authority for his information. As he omitted to list "*pseudoscutellaris*" from the Ellice Group in his Table "A", and his paper contains other inaccuracies such as the statements that *C. annulirostris* is absent from New Caledonia (where this species is common—Perry, 1950; Laird, 1954) and that *Aëdes* (*Stegomyia*) *tongae* Edw. is restricted to Tonga (it has been known from Sikaiana, Solomon Islands, for more than a quarter of a century—Edwards, 1926) Brygoo's record should be treated with reservation.

Finally, Buxton collected *Aëdes* (*Aëdimorphus*) *vexans* (Mg.) on the islands of Nui and Niutao in the Ellice Group (Buxton & Hopkins, 1927). It should be noted that Brygoo (1953) overlooked this record also. I cannot trace any record of *A. vexans* from the Gilberts, although Bohart & Ingram (1946) reported it from Ebon Atoll (Marshall Islands) to the north-west of the former Group.

It was stated in a U.S. Army Air Force wartime manual on tropical diseases (unpublished, 1944) that "*Aëdes kochi* is not found in the Fiji, Ellice, Cook and Phoenix Islands. In the Gilbert (Tarawa), Tokelau and Society Islands it breeds in coconut husks and other small collections of water". This is inaccurate. Apart from the fact that a representative of the *kochi* group does occur in Fiji—*Aëdes* (*Finlaya*) *fijiensis* Marks—*Finlaya* is unknown in the area under consideration (Stone & Bohart, 1944; Marks, 1947). The most easterly species of the *kochi* group is *A.* (*Finlaya*) *samoanus* (Grünb.), which occurs in Samoa and Tonga (Buxton & Hopkins, 1927). Larvae of *A. samoanus* are most frequently found in the water which collects in the leaf axils of certain species of taro (*Colocasia* and *Alocasia* spp.). Buxton & Hopkins drew particular attention to the absence of this species from the Ellice Islands, putting forward in explanation the facts that the brackish subsoil of these islands does not lend itself to the cultivation of the better types of taro and that the round-stem taro grown there does not hold water.

Discarding unsubstantiated records, then, the picture of mosquito distribution in the Gilbert, Ellice and Tokelau Islands presented by the literature is shown in Table I.

From time to time, flying boats of No. 5 Squadron, RNZAF, visit the Tokelau Group, Tarawa and Funafuti from Lauthala Bay, Fiji. The opportunity thus presented itself to collect material at each of these places in the course of routine flights. Although all the calls were brief ones, only a day being spent at Nukunono (Tokelau Group) and a similar period at Tarawa and at Funafuti, it is considered that the results achieved warrant publication.

TABLE I.

Species	Occurrence		
	Gilbert Is.	Ellice Is.	Tokelau Is.
A. aegypti	× −	× +	—
A. polynesiensis	—	× +	×
A. marshallensis	× +	—	—
A. vexans	— +	× +	—
C. annulirostris	— +	× +	—
C. pipiens fatigans	× −	—	—

TOKELAU GROUP.

A landing was made at Atafu on the afternoon of 15th June 1953, and a brief visit was paid to the village islet. Two collections of *scutellaris*-group larvae were made there, both of them from 44-gallon drums filled with rain-water of pH 7·0 and pH 6·4 at a temperature of 28°C. Ill-fitting wooden covers were present in both cases, and the drums were in the immediate vicinity of houses.

The aircraft reached Nukunono (09°10′S., 171°47′W.) later that afternoon. The population of this atoll at the last census was 452—226 males and 226 females. Thanks to the good offices of Father A. MacDonald and Sister Kasarina, who are stationed at Nukunono, 97 of these people, their ages ranging from 5 to 78, presented themselves for blood sampling. A single thick film was taken from the tip of the index finger of each individual, the survey being made between 1910 hr. and 2025 hr. on the evening of 15th June. The films were subsequently dehaemoglobinised and stained with Giemsa in the usual fashion. All those concerned had dwelt on the atoll for all, or for the greater part of, their lives.

The data obtained were inadequate for the estimation of any relationship between age and microfilaria concentration. Ten or more microfilariae were counted in the thick films from six individuals whose ages were 22, 25, 32, 34, 39 and 42 years. The heaviest concentration was noted for a man 34 years old, 30 microfilariae being present in his film.

In 1920, O'Connor examined 27 males, all over 16 years of age, at Nukunono. Four of these had microfilariae without clinical filariasis, one had both clinical filariasis and microfilariae and one had clinical filariasis alone. The microfilaria rate for this group was thus 18·5 per cent., while the overall percentage of infection was 22·2 per cent.

During the present survey, 28 males of over 16 years of age were examined (no notes on clinical filariasis being taken). Twelve of these exhibited microfilariae, the microfilaria rate thus being 42·9 per cent. The rates for 10-year age groups ranged from 28·6 per cent. for the 20–29 group to a maximum of

66·7 per cent. for the 50–59 group (Table II). In this connection, it is worth noting that Murray (1948) recorded the maximum percentage of microfilaria carriers in the 50–54 age group in American Samoa.

The total number of males above 16 years of age was only one more than that dealt with by O'Connor, but the microfilaria rates for each 10-year age group, as well as the overall rate, materially exceed the figure of 18·5 per cent. computed from the latter author's data. This might be due, at least in part, to a difference in techniques, for O'Connor based his conclusions on the examination of 20 cu. mm. of blood from each subject, and the volume of blood in the average thick drop is in excess of 20 cu. mm. Six of those examined in the present instance had relatively light infections, only one or two parasites being present in their films. Some or all of these infections might well have been overlooked had a smaller sample of blood been taken. Four of those concerned being men, the resultant microfilaria rate for males above 16 years of age could thus have been computed at 18·6 per cent.—a figure almost exactly comparable with O'Connor's. It cannot, therefore, be claimed that the microfilaria rate at Nukunono has increased since 1920, although the evidence now available indicates that this rate is higher than O'Connor estimated it to be.

TABLE II.

Microfilaria rate, Nukunono.

Age of persons (years)	Males			Females		
	Number examined	Positive		Number examined	Positive	
		No.	%		No.	%
1 — 9	7	0	0	5	0	0
10 — 19	8	0	0	11	0	0
20 — 29	7	2	28·6	14	2	14·3
30 — 39	6	2	33·3	7	1	14·3
40 — 49	5	2	40·0	10	1	10·0
50 — 59	6	4	66·7	5	1	20·0
60 plus	4	2	50·0	2	0	0
Total	43	12	27·9	54	5	9·3

Dr. J. S. Armstrong (Acting Director of Medical Services for Western Samoa at the time of this survey) informed me that two or three years ago he took 50 thick smears in the Tokelau Group, but that these, the only ones taken since O'Connor's visit, so deteriorated before staining as to be unsuitable for examination.

O'Connor examined more people at the other two atolls, Fakaofu and Atafu, than he did at Nukunono. Of a total of 330 individuals from all three atolls, 12 (of 85) under 16 years old and 90 (of 245) above that age showed evidence of infection. Only seven of those under 16 had microfilariae in their blood, the other five being what O'Connor called " doubtful cases of clinical filariasis ". Of the 90 above that age who showed signs of infection, 52 (of 145) were male and 38 (of 120) were female. However, 13 of the former and 22 of the latter were recorded as positive for filariasis on clinical grounds alone. Microfilariae were demonstrated for only 39 (26·9 per cent.) of the males and 16 (13·3 per cent.) of the females.

The microfilaria rate among Tokelau males is thus much higher than that among females, O'Connor's figures indicating a ratio of 2:1 and mine (Table II) one of 3:1. This is in accord with data available from American Samoa, where Murray (1948) found microfilariae in the blood of twice as many men as women above 20 years of age. It seems likely that this state of affairs is related, as previous authors have suggested, to the much greater amount of time which men spend working in the coconut plantations where the population of vector mosquitos of the *scutellaris* group is usually much greater than in the cleared ground about the villages where the women spend most of their time. Tokelau boys go regularly to the plantations (which are located on other islets than the village ones) from an early age. MacGregor (1937) stated: "Every family has a plantation of coconut trees on the atoll and usually some trees near the village. It is part of the young boys' work to keep the household supplied from these trees and to go with their fathers to the plantations two or three times a week and pick nuts."

Twelve larval habitats of mosquitos of the *scutellaris* group were located on 16th June. Seven of these were at Motusanga, a small islet covered with coconut palms at the southern end of the village islet, to which it is connected by a footbridge. The other five were on the village islet itself, this islet bearing the name of the atoll, Nukunono. Nine collections, five on Motusanga and four on Nukunono, were made at small reservoirs hollowed into the trunks of growing coconut palms (see O'Connor, 1923, Pl. IV, fig. 10; Buxton & Hopkins, 1927, Pl. XII, fig. A). Such tree reservoirs were formerly used to obtain drinking water, most of which is now stored in large concrete tanks. Thus the water in these cavities—at all events in those of them handy to the villages—is often allowed to lie untouched or is used by men returning from the lagoon, who dash it over themselves to wash away the salt. While six of the reservoirs examined teemed with larvae, three others, located near to the beach and thus in constant use, contained fewer larvae and many dead adults. Some of the latter were not fully free from the pupal pelt, and had apparently been knocked over in the act of emergence by mechanical disturbance of the water.

Two of the larval collections were made from rot-holes in a Puka tree (*Hernandia ovigera*) on Motusanga, while the remaining one was from water in the bottom of a beached canoe in the heart of Nukunono village. Adult males and females of the *scutellaris* group were found resting in the shaded upper parts of two of the tree reservoirs. A few females also emerged from some of the pupae collected. All the larvae collected at the atoll were typical of the *scutellaris* group, while the adults corresponded with the description of *Aëdes* (*Stegomyia*) *polynesiensis* Marks. Specimens were duly forwarded to Dr. Marks who confirmed my tentative identification (private communication, 1953).

The only other aquatic arthropods present in any of the mosquito breeding places were Ostracoda, discounting a crab, found at the bottom of one of the holes in the Puka tree, and identified as *Sesarma* sp., probably *rotundata* Hess, by Dr. C. H. Edmondson of the Bernice P. Bishop Museum, Honolulu. There were also a few Collembola on the surface film of some of the palm reservoirs. The hydrogen-ion content of the water in the last-named larval habitats ranged from 6·0 to 7·6 pH (av., 7·1), while that of the water in the Puka rot-holes was 6·8. In all cases the water temperature was much the same, varying from 26·25°C. to 27°C. The water in the beached canoe being very murky and of a deep yellow colour, a pH reading could not be taken by the only means available, a Lovibond comparator. All the breeding places were shaded from sunlight, the tree cavities by the part of the trunk above them and the canoe by a pile of palm fronds.

Two hours were spent in a fruitless search for mosquito larvae along the rubbish-strewn edges of a seepage pond some 50 yards in length and 20 yards in width, on Motusanga (fig. 1). The water there was brackish to the taste, with a pH content of 8·4. It is considered that this pond could support such a brackish-water breeder as *Culex* (*Culex*) *sitiens* Wied. should an introduction ever take place—as well it might, *C. sitiens* being common in Samoa, whence comes most of the (sporadic) shipping which visits the Tokelau Group.

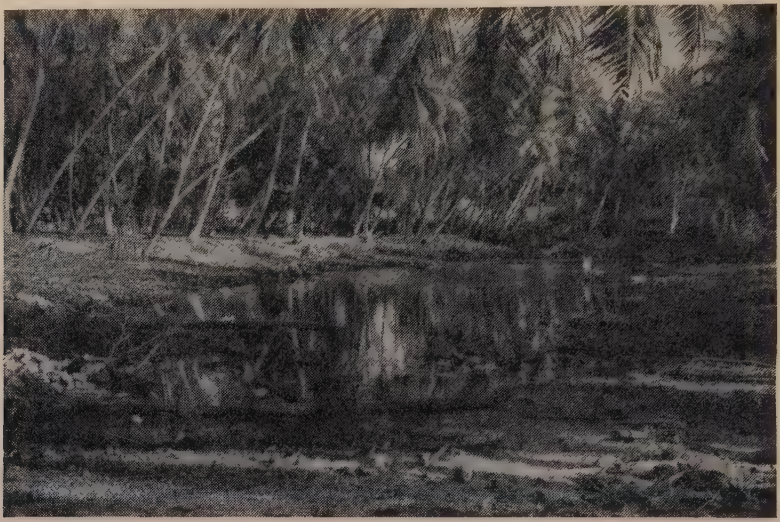


Fig. 1.—Brackish seepage pond, Motusanga.

No coconut shells holding water and suitable as breeding places could be found on Nukunono, a tribute to the state of cleanliness in which the village and its surroundings are maintained. No larvae of *A. polynesiensis* were found in 44-gallon drums as at Atafu, and an examination of the water held in 50 leaf axils of *Pandanus* disclosed no aquatic arthropods whatsoever. Night-biting mosquitos were conspicuous by their absence, although *A. polynesiensis* was troublesome in shady places both at Motusanga and on the village islet during the day.

TARAWA, GILBERT ISLANDS.

Mosquito collections were made at this atoll (01°30′N., 173°00′E.) on 27th January 1954. It was not practicable to undertake a blood-smear survey during the visit.

The domestic mosquitos, *Aëdes aegypti* and *Culex pipiens fatigans*, having already been recorded from Tarawa (p. 293), these were not searched for. Particular attention was paid to accumulations of surface water on the islets of Bairiki, Teaoraereke and Eita. The deep pits which the Gilbertese dig down to intersect the water table for the cultivation of their coarse taro or "babai" (*Cyrtosperma chamissonis*) proved of particular interest as larval habitats.

Larvae of *C. annulirostris* were found to be abundant on all three islets, being particularly common in the "babai" pits on Eita. There are some extensive pits on the latter islet, one of those examined measuring about 150 yd. by 100 yd.

and appearing to be an adapted natural swamp. During times of drought the seepage water in the "babai" pits is more or less brackish, but in the wet season—which was at its height at the time of this visit—so much rain-water is stored up that the resultant pools are all but fresh. The pH content of the water was found to vary between 7·2 and 8·0 (av., 7·4) at a temperature of 28°C. Larval Chironomids (identified by Dr. W. W. Wirth of the U.S. National Museum as *Tendipes* sp.) were usually present together with *C. annulirostris*, and the nymphs of Odonata (Anisoptera and Zygoptera) were always common. Great numbers of Collembola were noticed on the surface film of some small marginal pools. Other aquatic arthropods, notably Coleoptera and Hemiptera, appeared to be altogether lacking.

A brackish pond (pH 8·0 at 28°C.) near the beach at the eastern end of Teaoraereke supported huge numbers of the developmental stages of *C. annulirostris*. The entire surface of this pond, which measured 20 ft. by 15 ft., was literally black with larvae, despite the presence of large numbers of predators (dragonfly and damselfly nymphs). The species was also collected from flooded crab burrows. Adults of *C. annulirostris* were troublesome by night in the European houses on Bairiki.

One of the shallow pools in a rather dry "babai" pit on Bairiki proved to contain a few fully developed larvae of *Aëdes* (*Aëdimorphus*) *vexans nocturnus* (Theo.). Bohart & Ingram (1946) stated that larvae of the typical *A. vexans* (Mg.) have head hair B with two branches and C with three to five branches, whereas larvae from Australasia and the Philippines have B single and C single or double. On these grounds the Pacific representative of *A. vexans* was distinguished as *A. vexans nocturnus*. All the Tarawa examples seen have head hairs B and C both single, and are thus referred to this subspecies. No adults were collected.

A. marshallensis was common everywhere. Larvae abounded in the husks which littered the plantations, and imagines were a pest during the day-time in any shady patches of vegetation, particularly on Teaoraereke. The small pockets of water in 20 leaf axils of *Pandanus* were carefully searched for mosquito larvae, but as at Nukunono no arthropods of any kind were found.

Funafuti, Ellice Islands.

The afternoon of 29th January and the morning of the 30th were spent at Funafuti (08°28′S., 179°08′E.) on the way back to Fiji from Tarawa. As in the case of the latter atoll no blood-smears were made.

Collecting was confined to the largest islet, which bears the name of the atoll. The sandy soil of Funafuti is of much better quality than that of Tarawa. Pits, similar to those of the Gilbertese, are dug through the water table to make sunken gardens, some of which are of considerable size. The true taro (*Colocasia antiquorum* var. *esculenta*) is grown in addition to *Cyrtosperma chamissonis*. The Funafuti gardens were found to be much drier than those of Tarawa. Shallow pools in most of those examined held the aquatic stages of *A. vexans nocturnus* in association with larval Tipulids and Anisoptera, and amphipods, ostracods and freshwater snails. The pH content of the pools, like that of those at Tarawa, averaged 7·4 (range, 7·0 to 8·2). Water temperatures were higher than those recorded at the latter atoll, and in one instance that of a pool supporting a very heavy population of *A. vexans nocturnus* (up to 300–400 second-instar larvae per dip with a 200 cc. dipper) was as high as 37°C. (pH 8·2). Adults of this species were very troublesome at night-time.

A few adults of *C. annulirostris* were found resting in dark corners of a bedroom on the morning of the 30th. The only other record of this species at Funafuti was from the last-mentioned pool, and concerned an egg raft, from which larvae were just beginning to hatch.

Larvae and adults of a *Stegomyia* of the *scutellaris* group were common everywhere. Coconut husks lying about in the underbrush of the plantations often teemed with aquatic stages of this mosquito, which were also found in a small pool in a hollow on top of a knob of coral deeply shaded by overhanging vegetation. The pH content of the water in this larval habitat was 7·6 at 27·5°C. (the shade air temperature at the time was 28·5°C., while nearby pools in taro pits exposed to full sunlight averaged 33°C.; members of the *scutellaris* group are seldom found in water subject to marked temperature fluctuations, and the temperature of their larval habitats at the height of the day is usually less than the shade air temperature). Other larvae were found in a 44-gallon drum positioned so as to catch rain-water directed into it by means of a spout from the trunk of a coconut palm (pH 6·6 at 30°C.).

Imagines were extremely troublesome in the shade of the plantations. At one stage as many as 40 were present on my arms, and it was not possible to continue working without applying repellent. This is in marked contrast to the experience of O'Connor (1923), who declared that "I found only four or five specimens of *Stegomyia pseudoscutellaris* on this islet [*i.e.*, Funafuti.—M.L.], though *Culex jepsoni* [= *C. annulirostris*, see p. 292], which is absent from the other islets, is common". Perhaps the underlying reason is seasonal—O'Connor spent the driest months of the year (April–June) at Funafuti, and at that time a minimum of suitable mosquito breeding places would be available. As at Nukunono, the *scutellaris*-group mosquitos proved in every way comparable with the description of *A. polynesiensis*. Dr. Marks was sent material for checking, and once again she confirmed the identification (private communication, 1954).

The 44-gallon drum already mentioned contained numerous larvae of *A. aegypti* in addition to those of *A. polynesiensis*. No adults of *A. aegypti* were seen at Funafuti.

Many leaf axils of *Colocasia* and *Pandanus* were searched for mosquito larvae, once again with complete lack of success. Two to three hours were also spent in searching for mosquitos at the margins of two extensive brackish swamps (connected with the sea by underground channels, and thus subject to tidal action). Small pools in waterlogged ground at the edge of these swamps had a pH content of 10·0 at 32·5°C. Although outwardly suited to such brackish-water mosquitos as *C. sitiens*, these were quite without larvae.

Discussion.

The incidence of filariasis at Nukunono, as judged from the microfilaria rate, is appreciably higher than is apparent from O'Connor's (1923) results, and a much higher percentage of men than women exhibit *Wuchereria* there. Otherwise, the picture is substantially unchanged since 1920, no new mosquitos having made their appearance, although potential larval habitats for two Samoan species, *A. samoanus* and *C. sitiens*, are available at the atoll.

Tarawa and Funafuti have been the ports of entry to their respective Groups for many years. They are consequently the atolls most likely to be initially overrun by introduced mosquitos. On the available evidence it would seem that both *A. vexans nocturnus* and *C. annulirostris* have become established at Tarawa over the last quarter of a century. These species might well be very recent introductions, for in view of the military activity at Tarawa during World War II it is surprising that no mention of their presence was made in official survey reports. Both mosquitos could have been brought by sea or air from the Ellice Group, if not from further afield. *C. annulirostris* had become widely distributed in that Group by 1920 (O'Connor, 1923), while *A. vexans nocturnus* was present on at least two of the islands in 1924 (Buxton & Hopkins, 1927, as *A. vexans*). Although neither O'Connor nor Buxton found the latter insect on Funafuti it would have been an easy matter for them to have overlooked it, as their visits both took place during the dry season. *A. vexans nocturnus* is of sporadic occurrence throughout its area of distribution, typically appearing in huge numbers (often to the temporary exclusion of *C. annulirostris*) in temporary surface pools formed as a result of heavy rains. Finally, it is highly unlikely that the two authors in question, interested as they were in mosquitos utilising small natural and artificial containers as larval habitats, would have overlooked the presence of so important a domestic mosquito as *A. aegypti* at Funafuti.

Certain ecological niches suitable as mosquito larval habitats, although not as yet utilised by these insects, are available in the Gilbert and Ellice Islands. Conspicuous among these are the brackish swamps of Funafuti and leaf axils of *Pandanus* and *Colocasia*. As the lack of water-retaining taros in the Ellice Group was proposed by Buxton as a reason for the absence of *A. samoanus*, it can only be concluded that crop changes in recent years have laid the Group open to the possibility of a successful introduction of this annoying pest species.

Granted a suitable means of transportation, it is felt that the possibility of such an Anopheline as *Anopheles* (*Myzomyia*) *farauti* Lav. being introduced should not be overlooked. There is no reason why this dangerous mosquito should not be able to establish itself in the taro gardens of either Group.

Representative adults of *Aëdes polynesiensis* from Nukunono and Funafuti and of *A. marshallensis* from Tarawa have been deposited in the collection of the University of Queensland.

Summary.

It is confirmed that the *scutellaris*-group mosquito of the Tokelau and Ellice Islands is *Aëdes* (*Stegomyia*) *polynesiensis* Marks. No other mosquitos are known from the former Group, but *Culex* (*Culex*) *annulirostris* Skuse, *A.* (*Aëdimorphus*) *vexans nocturnus* (Theo.) and *A.* (*Stegomyia*) *aegypti* (L.) are also recorded from Funafuti, Ellice Islands. *C. annulirostris* and *A. vexans nocturnus* are listed—apparently for the first time—from Tarawa, Gilbert Islands. Reference is made to the microfilaria rate at Nukunono in the Tokelau Group, and to some potential mosquito larval habitats, as yet unutilised, in all three Groups.

Acknowledgements.

The Acting Director of Medical Services, Western Samoa, extended every assistance in connection with the visit to Nukunono, while the help afforded at that atoll by Father A. MacDonald was much appreciated. The collections in the Gilbert and Ellice Islands Colony were made with the approval of the Western Pacific High Commission and with the co-operation of the Acting Resident Agent at Tarawa and of the District Officer at Funafuti. I am grateful to my wife for her assistance in the field, and to Dr. E. N. Marks for examining the *scutellaris*-group mosquitos collected.

References.

Backhouse, T. C. & Heydon, G. A. M. (1950). Filariasis in Melanesia: observations at Rabaul relating to incidence and vectors.—Trans. R. Soc. trop. Med. Hyg., **44**, pp. 291–306.

Bohart, R. M. & Ingram, R. L. (1946). Mosquitoes of Okinawa and islands in the central Pacific.—NAVMED, no. 1055, 110 pp. Washington, D.C., Bur. Med. Surg., Navy Dep.

Brygoo, E. R. (1953). Epidemiology of filariasis in the South Pacific.—Filar. S. Pacif. Proc. Conf. Papeete, 1951, pp. 17–47. Nouméa, S. Pacif. Comm.

Buxton, P. A. & Hopkins, G. H. E. (1927). Researches in Polynesia and Melanesia . . . Parts I–IV.—Mem. Lond. Sch. Hyg. trop. Med., no. 1, 260 pp.

Davis, T. R. A. (1949). Filariasis control in the Cook Islands.—N.Z. med. J., **48,** pp. 362–370.

Edwards, F. W. (1924). A synopsis of the adult mosquitos of the Australasian Region.—Bull. ent. Res., **14,** pp. 351–401.

Edwards, F. W. (1926). Mosquito notes. VI.—Bull. ent. Res., **17,** pp. 101–131.

Laird, M. (1954). A mosquito survey in New Caledonia and the Belep Islands, with new locality records for two species of *Culex*.—Bull. ent. Res., **45,** pp. 285–293.

MacGregor, G. (1937). Ethnology of Tokelau Islands.—Bull. Bishop Mus., no. 146, 183 pp.

Marks, E. N. (1947). Studies of Queensland mosquitos. Part I.—Pap. Dep. Biol. Univ. Qd, **2,** no. 5, 66 pp.

Marks, E. N. (1951). The vector of filariasis in Polynesia: a change in nomenclature.—Ann. trop. Med. Parasit., **45,** pp. 137–140.

Murray, W. D. (1948). Filariasis studies in American Samoa.—Nav. med. Bull., **48,** pp. 327–341.

O'Connor, F. W. (1923). Researches in the western Pacific.—Res. Mem. Lond. Sch. trop. Med., no. 4, 59 pp.

Perry, W. J. (1950). The mosquitoes and mosquito-borne diseases on New Caledonia, an historic account: 1885–1946.—Amer. J. trop. Med., **30,** pp. 103–114.

Stone, A. & Bohart, R. M. (1944). Studies on mosquitoes from the Philippine Islands and Australasia (Diptera: Culicidae).—Proc. ent. Soc. Wash., **46,** pp. 205–225.

Venner, R. B. (1944). Filarial problem on Nanumea.—Nav. med. Bull., **43,** pp. 955–963.

Young, D. M. (1927). Gilbert and Ellice Islands Colony. Medical and Sanitary Report for the year 1925–26.—7 pp. Suva.

THE SUSCEPTIBILITY OF VARIOUS SPECIES OF MOSQUITOS TO DDT, DIELDRIN AND BHC.

By R. H. Wharton
Institute for Medical Research, Kuala Lumpur.

Although a vast body of literature has accumulated over the past few years dealing with the behaviour and mortality of mosquitos exposed to residual insecticides, there have been few attempts made to investigate differences in innate susceptibility. Experiments in window-trap huts of the type introduced by Muirhead Thomson (1948) have shown that DDT varies widely in its effect on different species of Anophelines and Culicines in various parts of the world. This is particularly true of Malayan mosquitos where Reid (1951) has recorded "a wide range of susceptibility to DDT, as if there is almost a complete reaction spectrum, with very susceptible species such as *Anopheles maculatus* at one end, and the least susceptible, such as *Culex fatigans* at the other." Field tests cannot, however, determine innate susceptibility since the degree of contact with an insecticide deposit will vary with different individuals of the same species and will vary widely with species having different feeding and resting habits.

A measure of innate susceptibility, then, is of obvious interest where differences in mortality have been observed under similar field conditions. But it is of even greater importance where the development of resistance to insecticides is suspected. In the present work an attempt has been made to measure the susceptibility of a number of mosquitos to DDT, BHC and dieldrin both as adults and as larvae, using techniques which could be reproduced with limited laboratory facilities. Experiments were commenced in London at the School of Hygiene and Tropical Medicine in 1952 and continued in 1953 and 1954 in Malaya at field laboratories in Tampin and Kuantan.

Materials and Methods.

The insecticides were prepared as solutions in a relatively non-volatile, non-toxic oil, Shell Risella Oil 17 (= P31 of Busvine & Nash, 1953) for adult tests, and as solutions in acetone for larval tests. Recrystallised p,p′DDT, γ BHC and a sample of technical dieldrin, 85 per cent. pure, were obtained through the courtesy of Dr. Busvine for experiments in London. Similar products of DDT and γ BHC and the same sample of dieldrin were used in Malaya. Concentrations of BHC refer to the γ isomer only.

Tests against adults.

Adult mosquitos were exposed to filter papers impregnated with varying concentrations of insecticide-oil solutions. Filter papers 11 cm. in diameter were treated in the afternoon, allowed to hang overnight and used the following morning. They were impregnated by the method of Busvine & Nash (1953); oil solutions of various strengths were prepared, diluted with twice the volume of ether, and 1 cc. of the resulting solution applied by means of a hypodermic syringe to a paper resting on pins. Since the insecticide remained in solution there was no problem of crystal size to consider. A strip was cut off one portion of the filter paper and was then rolled and placed in a flat-bottomed tube three inches high and one inch in diameter so that it lined the sides though not the bottom of the tube. The use of a tube was the only modification from the method of exposure used by Busvine & Nash (1953). Ten to twenty female mosquitos were removed from a cage with a suction tube, then blown gently into the tube and the top of the filter paper folded over. The mosquitos were exposed for one hour, then transferred to recovery cages and the mortality recorded after 24 hours.

For experiments in London the following species were available (with the conditions under which they were bred)—*Aëdes aegypti* (L.) (26°C., 80% R.H.), *Culex pipiens molestus* Forsk. (26°C., 70% R.H.), *Anopheles maculipennis* var. *atroparvus* van Thiel and *A. quadrimaculatus* Say (24–28°C. and 40–60% R.H.). Females two to three days old were fed on a guineapig and exposed 48 hours later in an incubator set at 30°C.; the recovery cages were maintained at 26°C. and 80 per cent. relative humidity.

For experiments in Malaya, *Aë. aegypti*, *Aë. albopictus* (Skuse), and *C. pipiens fatigans* Wied. (24–29°C. and 75–90% R.H.) were obtained from laboratory colonies; *Anopheles maculatus* Theo., *C. gelidus* Theo., *Mansonia longipalpis* (Wulp) and *M. uniformis* (Theo.) were caught in the field. Females were exposed at 26°C. approx., and the recovery cages were maintained at 24–29°C. and 75–90 per cent. relative humidity. Three- or four-day-old females of *Aë. aegypti* and *Aë. albopictus* blood-fed within the previous 24 hours, unfed *Aë. albopictus* and *C. p. fatigans* 3–4 days old, and *Anopheles maculatus*, *C. gelidus*, *M. longipalpis* and *M. uniformis* blood-fed within the previous 24 hours, were exposed. Experiments with *Aë. aegypti*, *Aë. albopictus*, *C. p. fatigans*, *C. gelidus* and *Anopheles maculatus* were carried out at a field laboratory at Tampin; others with *C. gelidus*, *M. longipalpis* and *M. uniformis* at a field laboratory at Kuantan.

Tests against larvae.

Larval mosquitos were exposed in 500 ml. glass beakers containing 250 ml. water to which various strengths of acetone solutions were added, to give the required concentration of insecticide in parts per million. The technique was very similar to that used by Trapido (1951); 245 ml. tap water was poured into each beaker, an appropriate amount of insecticide-acetone solution not exceeding 1 ml. was added and the suspension stirred with a glass rod. The beakers were then allowed to stand for one hour before batches of 25 early fourth-stage larvae from bowls containing 5 ml. water were added. Larvae of *Aë. aegypti*, *Aë. albopictus* and *C. p. fatigans* were obtained from laboratory colonies and tested when four days old; larvae of *Anopheles maculatus* were collected in the field. Tests commenced in the afternoon and were read the following morning, 20 hours later; all larvae dead, moribund or unable to perform normal movements were regarded as mortally affected. The tests were run at room temperature, which maintained the water at a temperature of 24–28°C.

Estimation of results.

The results were analysed by the probit method, following Finney (1952), in order to obtain median lethal concentrations (MLC). A number of tests were analysed by calculation of the regression equation and five per cent. fiducial limits, and are compared below with the MLC estimated visually from graphs.

Species	Insecticide	MLC (graph)	MLC (calc.)	5% fiducial limits
		Adults (% concentration)		
Aë. albopictus	DDT	1·27	1·27	1·11–1·46
Aë. albopictus	Dieldrin	0·23	0·24	0·21–0·26
A. maculatus	DDT	0·40	0·41	0·27–0·63
		Larvae (parts per million)		
Aë. aegypti	DDT	0·008	0·008	0·007–0·009
Aë. aegypti	Dieldrin	0·014	0·014	0·013–0·015
Aë. aegypti	BHC	0·060	0·065	0·058–0·073
Aë. albopictus	DDT	0·065	0·069	0·066–0·072

Graph estimates are used in discussion of all results.

Results.

Adults.

The results are summarised in Table I.

There was no striking difference in the susceptibility to DDT of the four species tested in London; *Aë. aegypti* (MLC 0·9 per cent.), *Anopheles m. atroparvus* (1·0) and *A. quadrimaculatus* (0·7) were of the same order, but *C. p. molestus* (1·6) was apparently less susceptible. *A. m. atroparvus* was more easily killed by dieldrin and BHC than was *Aë. aegypti* or *C. p. molestus*, which were about equal in susceptibility to these insecticides. Extremely low concentrations of γ BHC were lethal, indicating that this insecticide was far more toxic than dieldrin or DDT. This was to be expected since the fumigant properties of the fresh BHC deposit would be enhanced under the conditions of exposure. BHC was therefore excluded from Malayan tests against adult mosquitos.

The tests in Malaya revealed a much wider range of susceptibility to insecticides. The most significant finding was the low degree of susceptibility shown by *C. p. fatigans* to deposits of DDT. With the normal exposure of one hour, a concentration of 3 per cent. DDT killed all or nearly all the adults of other species tested, but no *C. p. fatigans*. Increase of the DDT concentration to 5 per cent. (the maximum concentration of DDT which could be obtained in the oil without rapid recrystallisation, and equivalent to a deposit of 163 mg. DDT per sq. ft.) gave a 4 per cent. mortality of *C. p. fatigans*. It was not possible, then, to obtain an MLC for *C. p. fatigans* using DDT and, for comparison with the other species, it has been recorded as greater than 5·0 per cent. It is worthy of note that when adults of *C. p. fatigans* were exposed continuously for 24 hours to 3 per cent. DDT, only about 50 per cent. were dead at the end of the exposure period.

Varying degrees of susceptibility to DDT were found with other species, ranging from *Anopheles maculatus* (MLC 0·4 per cent.) and *C. gelidus* (0·3 to 0·5) to *Aë. aegypti* (1·6) and *Aë. albopictus* (1·3), with the *Mansonia* species (0·5 to 0·8) intermediate.

Results with dieldrin again showed *C. p. fatigans* to be the least susceptible species, though it was readily killed by this insecticide (MLC 0·46 per cent.). Other species showed only small differences in susceptibility, with the MLC for *Aë. aegypti* and the *Mansonia* species virtually the same (0·12 to 0·14), and *C. gelidus* (0·18) and *Aë. albopictus* (0·23) rather less susceptible.

The most obvious inconsistency in these tests against adults is the difference in MLC for *Aë. aegypti* tested with DDT in London (0·9) and in Malaya (1·6). The tests against *Aë. aegypti* differed in that specimens in London were tested two days after feeding whereas Malayan specimens were tested only one day after feeding. Busvine (personal communication) has found that mosquitos are less susceptible shortly after feeding and this could possibly account for part of the difference. However, the MLC of London mosquitos is in good agreement with the results of Busvine & Harrison (1953) for *Aë. aegypti* from India and Africa. Difference in the temperatures at the time of exposure is a more likely reason for the lower susceptibility of Malayan specimens; the mosquitos were exposed at 30°C. in London and at 26°C. in Malaya, with the recovery cages held at about 26°C. in both places. Though DDT is generally more effective at low temperatures (Roth, Lindquist & Terriere, 1953), the results of Lindquist, Madden & Schroeder (1946) would suggest that, with short exposures, DDT is more lethal at higher temperatures; *e.g.*, 86 per cent. of *Anopheles quadrimaculatus* were dead after 24 hours when exposed to DDT for 15 minutes at 90°F. and kept at 70°F., compared with 20 per cent. dead when exposed at 70°F. Fay & others (1953) also record a greater mortality with higher testing and holding temperatures. A higher MLC would be expected, therefore, in the Malayan experiments.

TABLE I.

Adult mosquitos exposed for one hour to filter papers impregnated with various concentrations of insecticide-oil solutions. Percentage mortality after 24 hours (corrected).

(a) Tests in London

Insecticide	Species of mosquito	Number of replicates	Concentration of insecticide (%)														Median lethal concentration %
			0·003	0·006	0·01	0·018	0·03	0·06	0·10	0·18	0·3	0·6	1·0	1·8	3·0	5·0	
DDT	*Aë. aegypti*	4	—	—	—	—	—	—	—	—	7	21	58	88	—	—	0·9
	C. p. molestus	4	—	—	—	—	—	—	—	—	—	16	34	52	80	—	1·6
	A. m. atroparvus	4	—	—	—	—	—	—	—	—	—	32	46	66	92	—	1·0
	A. quadrimaculatus	4	—	—	—	—	—	—	—	—	21	33	74	100	—	—	0·7
Dieldrin	*Aë. aegypti*	4	—	—	—	—	—	—	21	62	97	100	—	—	—	—	0·13
	C. p. molestus	3	—	—	—	—	—	—	36	59	94	100	—	—	—	—	0·14
	A. m. atroparvus	3	—	—	—	—	29	59	75	97	100	—	—	—	—	—	0·05
γBHC	*Aë. aegypti*	4	—	13	35	80	97	100	—	—	—	—	—	—	—	—	0·013
	C. p. molestus	3	—	14	38	78	89	100	—	—	—	—	—	—	—	—	0·012
	A. m. atroparvus	2	11	28	58	95	100	—	—	—	—	—	—	—	—	—	0·008
(b) Tests in Malaya																	
DDT	*Aë. aegypti*	6	—	—	—	—	—	—	—	—	—	5	14	44	92	—	1·6
	Aë. albopictus	6	—	—	—	—	—	—	—	—	—	11	36	71	92	—	1·3
	Aë. albopictus (unfed)	6	—	—	—	—	—	—	—	—	11	50	88	100	—	—	0·6
	C. p. fatigans (unfed)	4	—	—	—	—	—	—	—	—	—	—	—	0	0	4	>5·0
	C. gelidus (Tampin)	5	—	—	—	—	—	—	—	—	45	74	91	100	—	—	0·3
	C. gelidus (Kuantan)	3	—	—	—	—	—	—	—	—	32	48	90	—	—	—	0·5
	M. longipalpis	4	—	—	—	—	—	—	—	—	11	33	59	92	—	—	0·8
	M. uniformis	4	—	—	—	—	—	—	—	—	25	60	76	94	—	—	0·5
	A. maculatus	4	—	—	—	—	—	—	—	—	45	58	88	100	—	—	0·4
Dieldrin	*Aë. aegypti*	3	—	—	—	—	—	15	36	74	100	100	—	—	—	—	0·13
	Aë. albopictus	6	—	—	—	—	—	—	13	33	62	95	—	—	—	—	0·23
	C. p. fatigans (unfed)	5	—	—	—	—	—	—	—	2	15	81	95	—	—	—	0·46
	C. gelidus (Kuantan)	3	—	—	—	—	—	12	26	47	69	—	—	—	—	—	0·18
	M. longipalpis	4	—	—	—	—	—	—	23	62	97	—	—	—	—	—	0·14
	M. uniformis	4	—	—	—	—	—	11	39	77	97	—	—	—	—	—	0·12

TABLE II.

Larval mosquitos exposed to various concentrations of insecticide-acetone suspensions in Malaya.
Percentage mortally affected after 20 hours (corrected).

Insecticide	Species of mosquito	Number of replicates (25 larvae)	Concentration of insecticide (parts per million)									Median lethal concentration (parts per million)
			0·001	0·0025	0·005	0·01	0·025	0·05	0·1	0·25	0·5	
DDT	*Aë. aegypti*	6	—	7	27	58	95	99	—	—	—	0·008
	Aë. albopictus	8	—	—	—	—	14	41	67	94	—	0·065
	C. p. fatigans	6	—	—	—	—	0	15	47	63	87	0·145
	A. maculatus	4	—	—	7	27	37	71	92	—	—	0·026
Dieldrin	*Aë. aegypti*	8	—	0	5	36	78	98	—	—	—	0·014
	Aë. albopictus	6	—	0	7	26	60	94	—	—	—	0·020
	C. p. fatigans	8	4	33	81	99	100	—	—	—	—	0·003
	A. maculatus	3	10	37	65	89	100	—	—	—	—	0·0034
γBHC	*Aë. aegypti*	6	—	—	—	3	12	28	69	99	—	0·060
	Aë. albopictus	6	—	—	—	—	—	9	59	97	100	0·098
	C. p. fatigans	8	—	3	10	45	70	100	—	—	—	0·014
	A. maculatus	4	—	—	—	6	15	32	92	100	—	0·047

There remains also the possibility that Malayan *Aë. aegypti* are of a less susceptible strain. This suggestion finds some support from the results of a small-scale DDT residual house-spraying programme in Port Swettenham, Malaya, where *Aë. aegypti* is still present in houses after several applications of DDT over a period of two years (J. A. Reid, personal communication), whereas reports from other parts of the world, *e.g.*, British Guiana and Mauritius, indicate that *Aë. aegypti* was virtually eradicated after one application of DDT in houses.

Attention must be drawn to the fact that unfed *C. p. fatigans* were used for most experiments. The few fed specimens available from the laboratory colony showed a similar lack of susceptibility to DDT deposits, and when fed and unfed *Aë. albopictus* were exposed to DDT it was found that unfed specimens (MLC 0·6 per cent.) were much more susceptible than fed specimens (1·3). It seems most unlikely, therefore, that the use of unfed *C. p. fatigans* was responsible for the low degree of susceptibility encountered, and quite probable that adequate tests with fed specimens would show them to be even less susceptible.

Larvae.

The results are summarised in Table II. Larvae of different species showed considerable variation in susceptibility to specific insecticides but the most obvious finding was the low degree of susceptibility of *C. p. fatigans* to DDT. In the larval stage, this species was much more difficult to kill by DDT (MLC = 0·145 parts per million) than *Aë. aegypti* (0·008), *Aë. albopictus* (0·065) or *Anopheles maculatus* (0·026), but was more easily killed than any other species by both dieldrin and BHC. There was no constant relationship between the species tested and its susceptibility compared with other species, *e.g.*, *Aë. aegypti* was the most susceptible to DDT, but more difficult to kill by dieldrin or BHC than *C. p. fatigans* or *Anopheles maculatus*.

Comparative Toxicity of DDT, Dieldrin and BHC.

Table III indicates the comparative toxicities of DDT, dieldrin and BHC to different species of mosquitos. They are in general agreement with those recorded in other investigations (Busvine, 1952; Busvine & Nash, 1953).

TABLE III.

Potency of dieldrin and BHC to various mosquitos relative to DDT (= 1·0).

Species	Adults		Larvae	
	Dieldrin	BHC	Dieldrin	BHC
Aë. aegypti	7–12	69	0·6	0·13
Aë. albopictus	6	—	3·2	0·65
C. p. fatigans	>11	—	48·0	10·40
C. p. molestus	11	133	—	—
C. gelidus	2–3	—	—	—
M. longipalpis	6	—	—	—
M. uniformis	4	—	—	—
A. m. atroparvus	20	125	—	—
A. maculatus	—	—	7·7	0·55

Against adult mosquitos, dieldrin is clearly much more toxic to all species than is DDT, and apart from *Aë. aegypti* the same is true for larvae. BHC appears as the most toxic material to adults; this was to be expected since it was the only insecticide tested which acts as a fumigant and this property would be enhanced under the conditions of the test. As a larvicide, BHC is less potent to all species than is dieldrin, and excluding *C. p. fatigans*, it is also less potent than DDT.

Discussion.

Many observers have found that DDT is more effective against some species of mosquitos than against others under field conditions. The results presented in this paper show that there may be marked differences in susceptibility to insecticides between the adults and larvae of various species exposed under similar conditions in the laboratory. The most striking example is the extremely low degree of susceptibility of adult *C. p. fatigans* to DDT. It is well known that this species, domestic in habit, is not controlled by spraying DDT in houses (Giglioli, 1948; Davidson, 1952), though activated by the DDT and driven out of houses (Wharton, 1951). Since recent experiments by Hadaway & Barlow (1953) suggest that there is no marked difference in the rate at which mosquitos are activated by DDT, the low degree of susceptibility observed in the present work is not surprising. There is no reason to suspect that it is an acquired resistance to DDT.

Results with *C. gelidus* are of particular interest since this species was tested against DDT at two widely separated places using specimens caught in the field. A comparatively small difference in median lethal concentrations was obtained, 0·3 per cent. at Tampin and 0·5 per cent. at Kuantan. Considering the crude methods of exposure, this small difference is reassuring. The high degree of susceptibility of *C. gelidus* to DDT is also of interest, for both *C. p. molestus* and *C. p. fatigans*, belonging to the same genus, were found to be less susceptible than mosquitos of other genera tested in England and Malaya.

Little purpose is served by a comparison of Malayan results with those obtained with different mosquitos in other countries. Comparable tests with adults have not been recorded elsewhere except for *Aë. aegypti*, and larval tests cannot be expected to show close correlation, even with the same species, when conditions of breeding and exposure are not absolutely standardised. Allowing for such variations, the median lethal concentrations of DDT determined for larvae of *Aë. aegypti* in Malaya, 0·008 p.p.m., and the United States, 0·003 (Deonier & others, 1949) are not unduly different.

What is more important is that, in each area where insecticides are used, some attempt should be made to determine the susceptibilities of the vector mosquitos. Results of such tests should permit a rational choice of insecticide according to the species and stage to be controlled, and should serve as bases of comparison if resistance is suspected. The measure of susceptibility should be in terms of a median lethal dose or concentration.

Summary.

The susceptibility of various mosquitos to DDT, dieldrin and BHC has been studied. Adult females were exposed in small tubes lined with filter papers impregnated with insecticide-oil solutions. Larvae were exposed to insecticide-acetone suspensions in water.

Adult mosquitos tested in London showed no striking differences in susceptibility to DDT, though the median lethal concentration (MLC) of *Culex pipiens molestus* Forsk. (1·6 per cent.) was greater than the MLC of *Aëdes aegypti* (L.) (0·9), *Anopheles maculipennis* var. *atroparvus* van Thiel (1·0), or *A. quadrimaculatus* Say (0·7). *C. p. molestus* and *Aë. aegypti* showed the same order

of susceptibility to dieldrin and BHC, with *Anopheles m. atroparvus* more susceptible to both insecticides.

Adult and larval mosquitos in Malaya varied considerably in their susceptibilities to DDT, dieldrin and BHC. Adult *Culex pipiens fatigans* Wied. showed a low degree of susceptibility to DDT (MLC>5·0) and other species showed varying degrees of susceptibility, *Aë. aegypti* (1·6), ~~*Anopheles*~~ *albopictus* (Skuse) (1·3), *Mansonia longipalpis* (Wulp) (0·8), *M. uniformis* (Theo.) (0·5), *C. gelidus* Theo. (0·3 to 0·5) and *Anopheles maculatus* Theo. (0·4). *C. p. fatigans* (0·46) was readily killed by dieldrin, but was less susceptible than *Aë. albopictus* (0·23), *C. gelidus* (0·18), *M. longipalpis* (0·14), *Aë. aegypti* (0·13) or *M. uniformis* (0·12). Larvae of *C. p. fatigans* (MLC 0·145 parts per million) were also less susceptible to DDT than *Aë. aegypti* (0·008), *Aë. albopictus* (0·065), or *Anopheles maculatus* (0·026); but were more easily killed by dieldrin and BHC than the other species.

ë.

Under the conditions of these experiments BHC was apparently the most toxic material to adults because of its fumigant properties. Dieldrin was found to be more toxic than DDT to the adults of all species. Dieldrin was the most effective material against larvae; it was more toxic than BHC to all species and more toxic than DDT to all except *Aë. aegypti.* DDT was more toxic than BHC to the larvae of all species except *C. p. fatigans.*

It is suggested that, where possible, a median lethal concentration should be determined for the main vector mosquitos wherever residual insecticides are used, to serve as a basis for comparison when resistance is suspected.

Acknowledgements.

I am grateful to Professor P. A. Buxton for his permission to work in the Entomology Department of the London School of Hygiene and Tropical Medicine and to use mosquitos from the departmental stock colonies. Dr. J. R. Busvine of the same Department was extremely helpful in many ways, particularly in deciding technique for adult tests. I am indebted also to the Malayan Government for a grant of study leave which enabled me to work in the United Kingdom.

References.

Busvine, J. R. (1952). The newer insecticides in relation to pests of medical importance.—Trans. R. Soc. trop. Med. Hyg., **46**, pp. 245–254.

Busvine, J. R. & Harrison, C. M. (1953). Tests for insecticide-resistance in lice, mosquitos and house-flies.—Bull. ent. Res., **44**, pp. 729–738.

Busvine, J. R. & Nash, R. (1953). The potency and persistence of some new synthetic insecticides.—Bull. ent. Res., **44**, pp. 371–376.

Davidson, G. (1952). Experiments on the use of DDT, BHC and dieldrin against adult mosquitoes at Taveta, Kenya.—Nature, Lond., **170**, pp. 702–703.

Deonier, C. C., Raun, E. S., Peek, E. H., Davis jr., A. N. & Nottingham, E. (1949). A comparison of DDT and other new insecticides for mosquito control.—Mosq. News, **9**, pp. 150–152.

Fay, R. W., Kilpatrick, J. W., Crowell, R. L. & Quarterman, K. D. (1953). A method for field detection of adult-mosquito resistance to DDT residues.—Bull. World Hlth Org., **9**, pp. 345–351.

Finney, D. J. (1952). Probit analysis.—2nd edn., 318 pp. Cambridge, Univ. Press.

Giglioli, G. (1948). Malaria, filariasis and yellow fever in British Guiana.—226 pp. [Georgetown] Mosq. Contr. Serv., Med. Dep., Brit. Guiana.

Hadaway, A. B. & Barlow, F. (1953). Studies on aqueous suspensions of insecticides. Part IV. The behaviour of mosquitos in contact with insecticidal deposits.—Bull. ent. Res., **44**, pp. 255–271.

Lindquist, A. W., Madden, A. H. & Schroeder, H. O. (1946). Effect of temperature on knock-down and kill of mosquitoes and bedbugs exposed to DDT.—J. Kans. ent. Soc., **19**, pp. 13–15.

Muirhead Thomson, R. C. (1948). Studies on *Anopheles gambiae* and *A. melas* in and around Lagos.—Bull. ent. Res., **38**, pp. 527–558.

Reid, J. A. (1951). Effects of DDT upon different species of mosquitoes in Malaya.—Nature, Lond., **168**, pp. 863–865.

Roth, A. R., Lindquist, A. W. & Terriere, L. C. (1953). Effect of temperature and the activity of house flies on their absorption of DDT.—J. econ. Ent., **46**, pp. 127–130.

Trapido, H. (1951). The toxicity of DDT to *Anopheles claviger* (Meigen) in Sardinia and on the Italian mainland.—J. nat. Malar. Soc., **10**, pp. 266–271.

Wharton, R. H. (1951). The behaviour and mortality of *Anopheles maculatus* and *Culex fatigans* in experimental huts treated with DDT and BHC.—Bull. ent. Res., **42**, pp. 1–20.

ERRATA

Solomon & Adamson, Bull. ent. Res. 46 (1955).

p.327. Hut 49 is on Pl. XII, not XI.

p 335. The second par. under CARYEDON FUSCUS should be transferred to ORYZAEPHILUS SURINAMENSIS, p.339.

THE POWERS OF SURVIVAL OF STORAGE AND DOMESTIC PESTS UNDER WINTER CONDITIONS IN BRITAIN.

By M. E. Solomon and Betty E. Adamson

E.M./

Department of Scientific and Industrial Research,
Pest Infestation Laboratory, Slough, Bucks.

(Plates XI & XII.)

Contents.

	PAGE
Introduction	311
Variable Factors affecting Success in Overwintering	313
Cold-hardiness	313
Effects of previous conditions	314
Differences between strains or races within a species	315
Period of exposure	315
Moisture conditions	315
Severity of the winter	316
Type of building	318
Protection afforded by materials in storage	320
Heating of the immediate environment	322
Systematic List of Species	323
Methods and Procedure	325
Preparation of the insects	325
Exposure of the insects	325
Observation of the insects	325
Recording of temperature and humidity	326
Comparison of different exposures	326
Results	330
Detailed Comments on Results	331
General Discussion	344
Summary	348
Acknowledgements	349
References	350

Introduction.

In assessing the actual and potential significance of a pest, its ability to survive the seasonal changes in physical conditions in the habitat is a major consideration. In Britain, the difficult season for most insects is the winter. If an introduced pest cannot survive the cold weather, its scope as a permanent inhabitant will be severely restricted.

As far as pests of stores and houses are concerned, a good deal of general knowledge has been accumulated in Britain, particularly by the Grain Survey team (Munro, 1940), by the entomologists and inspectors of the Infestation Control Division, Ministry of Agriculture, Fisheries and Food, and by the staff of the Pest Infestation Laboratory. Some of this information can be found in various publications, such as those by Freeman (1948*a*, *b*), Freeman & Turtle (1947) and O'Farrell & Butler (1948).

Freeman (1948*a*) distinguishes three groups of storage pests on the basis of their relative susceptibility to cold. In the first group, of species able to survive the British winter in unheated buildings, he includes the larvae of the Cacao Moth, *Ephestia elutella* (Hb.), the adults of the Grain Weevil, *Calandra granaria* (L.), and *Ptinus tectus* Boield. and other Spider Beetles. The more complicated groupings of O'Farrell & Butler (1948) are only partly based on cold-resistance; the species which are explicitly or implicitly stated to survive the winter in unheated buildings in N. Ireland include the moths *Endrosis lactella* (Schiff.) (= *sarcitrella* (L.)), *Hofmannophila pseudospretella* (Stnt.) and the common British Tineid pests; the Ptinid beetles; *C. granaria*, *Oryzaephilus surinamensis* (L.),*Tenebrio molitor* L., *Palorus* spp., *Tenebroides mauritanicus* (L.), *Lepisma saccharina* L.; the mould-feeding beetles *Cryptophagus* spp., *Enicmus minutus* (L.) and *Mycetaea hirta* Marsham; and various carnivores including some Staphylinid beetles, some Carabids of the genus *Pristonychus*, and *Blaps mucronata* Latr., *Dermestes lardarius* L., *Attagenus pellio* (L.), and the bug *Lyctocoris campestris* (F.).

In Freeman's second group, of insects unable to survive the British winter in unheated buildings, he mentions the beetles *Araecerus fasciculatus* (Deg.), *Rhizopertha dominica* (F.), *Tribolium castaneum* (Hbst.), and the moths *Corcyra cephalonica* (Stnt.) and *Sitotroga cerealella* (Ol.). We may add a number of beetles from O'Farrell & Butler (*loc. cit.*), namely *Alphitobius diaperinus* (Panz.), *Calandra oryzae* (L.), *Gnathocerus cornutus* (F.), *Laemophloeus ferrugineus* (Steph.), *L. minutus* (Ol.), *Oryzaephilus mercator* (Fauv.), *R. dominica*, *Tenebrio obscurus* F. and *Tribolium confusum* Duv. The results of our experiments show that *L. ferrugineus*, *S. cerealella* and *T. obscurus* should be excluded from this group, and there is some doubt about *A. diaperinus*. Freeman excludes *C. oryzae*.

Freeman distinguishes a third, intermediate group of "species which are borderline cases, surviving under specially favourable conditions in warmer parts of the country; these include *Necrobia rufipes*, *Ephestia cautella*, and *Calandra oryzae* ".

Of course, as Freeman remarks, in heated buildings species can survive the winter which cannot do so in warehouses; also the production of heat by heavy infestations is a factor enabling certain species to overwinter; and finally, he mentions the heat-conserving properties of bulk grain, in virtue of which the deeper parts may remain warm through the winter and so provide for the survival of certain insects.

These are some of the variables affecting the temperatures which storage pests may experience in the course of a winter. Together with other factors, they will be discussed in the following pages. These variable factors add to the difficulty of keeping the above classification to clearly defined lines, and make the subject of overwintering necessarily complex. A second general difficulty at present is the paucity of information about the powers of resistance of most of the species. There is an obvious need for more detailed observations and more precise knowledge.

An experimental study of the problem was made by Mansbridge (1936), who exposed cultures of 42 species of storage pests to winter conditions in an unheated building. He presented his results together with a record of the weekly maxima and minima of temperature and humidity. His data have been a valuable guide to everyone concerned with the ecology of these pests.

Somewhat similar experiments were conducted by Mathlein (1938) with *C. granaria* and *C. oryzae*.

The present work is essentially a continuation and development of Mansbridge's experiments. It was thought desirable to test the effects of a greater range of weather than that provided by the two winters in which Mansbridge worked, to extend the tests to more species, as well as checking some of the more critical results, also to study the effects of different types of buildings in modifying the temperature. We have made special efforts to get detailed and reliable temperature records.

From the physiological point of view, it would be more interesting to make a close study of the cold resistance of one species. But for economic and for many ecological problems we need to know, in much more detail than hitherto, how much exposure to cold is undergone by insects in various situations, and how much they can survive. This applies more particularly to those species which sometimes fail to overwinter. For such species the picture is rather complex, owing to the variation of a number of different factors which are discussed below.

Variable Factors Affecting Success in Overwintering.

The main factors are:— (a) cold-hardiness, (b) effects of previous conditions, (c) differences between strains or races within a species, (d) period of exposure, (e) moisture conditions, (f) severity of the winter, (g) type of building, (h) protection by materials in storage, (i) heating of the immediate environment.

Cold-hardiness.

Most insects are killed when their bodies freeze, although some can survive solidification if the temperature is not too extreme and so long as the freezing is only extra-cellular (Asahina, Aoki & Shinozaki, 1954). Freezing occurs at various temperatures appreciably lower than 0°C. (Salt, 1936) after an exposure period which often varies a good deal between individuals of a species (Salt, 1950). Some insects, including many of the storage pests introduced from warmer countries, will die of cold even at temperatures above 0°C. In neither case is the precise cause of death from cold understood, although various hypotheses have been advanced (*cf.* Wigglesworth, 1950, p. 443). But it is clear that the intensity of cold and the duration of exposure are both important factors affecting survival.

When an insect is exposed to cold its movements become slower than at normal temperatures. It may be reduced to a state of cold stupor, or chill coma, *i.e.*, practically all movement ceases and the metabolic rate is greatly reduced. Some species, under the appropriate conditions, lapse into a state of hibernation, in which the metabolic rate falls to an extremely low level and their cold-hardiness is considerably increased.

Neither cold stupor nor hibernation will enable an insect to survive if the cold is too extreme, or too prolonged. With long exposures, insects which escape direct consequences of the cold, such as freezing of the tissues or the fatal blocking of vital processes, will die of starvation if the temperature does not rise before their reserves are exhausted. Hibernating insects can continue for very long periods before this happens. Possibly other causes of death also operate in such circumstances.

The distinction between mere stupor and hibernation is not always clear. Hibernation may be preceded by a building up of food reserves and a loss of water from the tissues. There is a marked increase in cold-resistance in the hibernating condition. Hibernation often has the characteristics of a diapause, so that an insect cannot recover from it in response to a rise in temperature until certain conditions (such as a minimum period of exposure to low temperature) have been fulfilled. Such relationships are often important in preventing the premature emergence of cold-susceptible stages during mild spells.

The gist of the literature on the above points is given by Salt (1936), Imms (1937), Allee & others (1949) and Wigglesworth (1950).

Salt (1953) finds that the resistance of larvae of *Agrotis orthogonia* Morr. and

Ephestia kuehniella Zell. to freezing is greater when there is no food in the gut. He maintains that neglect of this factor, and of the influence of contact moisture, invalidates many earlier experiments on cold-resistance.

As far as storage pests are concerned, it would be interesting to know how far different species can develop cold-hardiness as a result of exposures to low temperatures. Cotton (1949) states that *Tineola bisselliella* (Humm.) becomes more resistant to cold as a result of exposure and also that *Tenebroides mauritanicus* in a farm store became more resistant to cold (and to heat) with the onset of autumn.

The effect of a gradual as compared with a sudden approach to a lethal low temperature was investigated by Robinson (1926), working with *C. oryzae*. He found that, instead of developing cold-hardiness, the beetles which had been brought by gradual stages to the low temperature were a good deal less resistant than those which had been exposed suddenly. The series of short exposures to decreasing temperatures, though not lethal, had in effect prolonged the harmful exposure to cold. Ushatinskaya (1948) attributed this result of Robinson's to the fact that his beetles had been bred on grain of unfavourably low moisture content (13–14%), and pointed to the poor cold-resistance of his *C. oryzae* and *C. granaria* compared with the figures of other authors (*cf.* p. 334, also fig. 4). In her own experiments with *C. granaria*, beetles exposed to various low temperatures from about 0°C. to −15°C. died sooner after a rapid transference to the low temperature than after a gradual reduction. A rapid transference back to a higher temperature had no more effect than a gradual transition.

Repeated short exposures to a low temperature may be more harmful than continuous exposure. In an experiment with *Trogoderma granarium* Everts, Voelkel (1924) took larvae reared at 25°C., and held them for periods of one hour at each of the temperatures 18°, 12°, 4°, 0°C., in that order. They were then removed to −10°C. for 20 hours, then returned by similar stages to 12°. This was repeated for two more cycles, the times at −10°C. being 3 hours and 2 hours. This treatment, involving a total of 25 hours at −10°C., killed 73 per cent. of the larvae, whereas continuous exposure for 72 hours at this temperature killed only 11 per cent.

On the other hand, any harmful effects of short non-lethal exposures tend to disappear on return to higher temperatures, so that the effects of successive exposures to cold are not cumulative if they are not too sudden and if adequate recovery periods are allowed. Robinson (1926) exposed adults of *C. oryzae* for 24 hours at −1·1°C., which killed 32 per cent. of them, kept the survivors under favourable conditions for a week, and then found that they had recovered their original resistance (in fact, had exceeded it: a result attributed to the favourable conditions enjoyed between the two tests).

Effects of previous conditions.

We have noted that *Tineola bisselliella* and *Tenebroides mauritanicus* are said to become more resistant to cold as a result of exposure to it. Rearing conditions are also likely to affect cold-hardiness. Payne (1934) reported that adults of the parasite *Bracon hebetor* Say reared at low temperatures withstood −12°C., while those reared at high temperatures died at −7° to −8°C. Mellanby (1939) found that adults of *Blatta orientalis* L. taken from 30°C. were killed by exposure to −5·5°C. for 1 hour, whereas those taken from 15°C. required 10 hours at −8°C. Colhoun (1954) has found that *Blattella germanica* (L.) acclimatised at 15°, 25° and 35°C. survive longer at 7°C., the lower the acclimatisation temperature. The testing of other storage pests in this way is a large field awaiting investigation.

Since our experiments were not designed for the study of such phenomena, it was desirable to avoid possible variations due to differences in the conditions prior to the experiment. Most of the insects were reared under a standard set of conditions of temperature and humidity, and the experimental cultures were held under these conditions for a time (usually a week or two) before the start of each test.

Differences between strains or races within a species.

When distinguishable strains or races of a species exist, it is likely that they will differ to some extent in their resistance to cold. The two strains of *E. kuehniella* investigated by Payne (1934), one of which develops much more rapidly than the other, also have different thresholds of development, 8°C. for the slow strain and 10°C. for the fast one. Payne did not otherwise compare the cold-resistance of the two strains. She cited figures suggesting considerable differences between the resistance of stocks from different climatic areas, but did not indicate whether or not these differences might have been attributable to the effects of the varied conditions experienced by the insects before the tests.

The large and small strains of *C. oryzae* differ in their rates of development (Richards, 1944), but their relative resistance to cold has not been studied, nor has that of the two strains of *T. molitor* which Leclercq (1950) separated from a single stock. In the course of the present work, we have found that our insectary stock of *C. granaria* is distinctly more susceptible to cold than the stocks tested by some other workers; we have not determined whether this is a transient effect of differences in culture conditions, or whether more permanent genetic differences are involved. Most species have not been sufficiently studied to show whether or not they comprise distinguishable strains, except where there are marked morphological differences, as in the four varieties of *Anthrenus vorax* Waterh., distinguishable by the colour pattern (Hinton, 1945).

It is likely that certain of the groups at present given specific names will ultimately turn out to be multispecific. The name *Attagenus piceus* (Ol.) has been widely applied to at least two distinct forms, probably species (Zinkernagel, 1952). Our insectary stock of "*Tinea pellionella*" was found to contain also another closely similar species, *Tinea columbariella* Wocke (Woodroffe, 1950).

Period of exposure.

We have noted above (p. 313) the importance of duration of exposure in determining survival or death. While a very short exposure may be sufficient to kill an insect at very low temperatures, the exposure periods necessary to kill susceptible insects at temperatures around 0°C. are generally to be measured in days or weeks.

In most of our experiments the insects were exposed from November to April (inclusive). This does not mean, of course, that they were exposed to harmful temperatures throughout the period. What they experienced was an irregular series of cold periods of varying intensity and duration. For a number of species the temperature never approached a harmful degree of cold.

Some experiments were run over shorter periods to test the resistance of non-overwintering species to briefer exposures. The aim of these tests was to supplement earlier information and also to throw light on the practical question of the ability of certain species to survive on to the warmer season if imported in the latter part of the winter.

Moisture conditions.

The effect of moisture content of the insects as a factor in survival (at lower temperatures than we are concerned with here) was investigated by Salt (1936), who got results which varied a great deal between different species. Working with *C. granaria* and *C. oryzae*, Robinson (1926) found that both were much more resistant (to temperatures of −12·2° and −1·1°C. respectively) when they had been kept on wheat of higher moisture content. Ushatinskaya (1950*b*) showed that the resistance of *C. granaria* to various temperatures from 0°C. downwards increased with the moisture content of the grain. But with *L. minutus*, Williams (1954) tested the cold-resistance of eggs and adults at relative humidities from 35 to 88 per cent., and found no difference due to humidity.

In the present experiments the atmospheric humidity was not controlled. Generally the relative humidity fluctuated about a level near 80 per cent., not often going beyond the range 70 to 90 per cent.

Severity of the winter.

Among the variables to be borne in mind when drawing any general conclusion about the overwintering capacity of a species, we must consider the range of variation of British winters, both from year to year and between different parts of the country.

As an example of the variability of winter temperatures from year to year, we may take the figures for Kew in January, as given by Bilham (1938, p. 170). For the period 1871–1935, the January mean varied between 31·7° and 45·8°F. (−0·2° to 7·7°C.). The mean daily *minimum* temperature for January averaged 34·6°F. (1·4°C.) over the period 1881–1915; in 1881 it was as low as 27·3°F. (−2·6°C.), and on one day the temperature fell to 9°F. (−12·8°C.).

Some idea of the variation from place to place is given by Bilham's map (p. 156) with isotherms for January mean temperatures. These range from nearly 46°F. at Land's End to somewhat below 40°F. in (very roughly) the eastern half of England and Scotland. This map has been simplified by raising the temperature figures to values corresponding to sea level, at the rate of 1°F. per 300 ft.

For the present purposes the severity of a winter may be assessed in various ways. The choice of a procedure should be determined by a knowledge of the

TABLE I.

Data for an estimate of the relative severity of the winters in which our experiments and those of Mansbridge (1936) were done.

Winter (Nov.–Apr. inclusive)	Mean daily minimum temperatures in 3 coldest months* °C.	Deviations in °C. of mean daily temperatures for each month from average values					
		Nov. 6·8	Dec. 5·2	Jan. 5·2	Feb. 5·1	Mar. 6·6	Apr. 8·7
1934–35	4·0 (Jan., Mar., Feb.)	+0·4	+3·7	−0·2	+1·7	+0·5	+0·2
1949–50	3·3 (Feb., Jan., Nov.)	+0·1	+1·5	−0·3	(+1·6)	+1·7	0
1951–52	2·5 (Feb., Jan., Mar. or Dec.)	+2·4	+1.3	−1·2	−1·2	+0·7	+1·9
1935–36	2·2 (Feb., Dec., Jan.)	+1·1	−1.0	−0·4	−1·7	+1·2	−1·4
1953–54	1·8 (Feb., Jan., Apr.)	+1·5	+3·2	−1·1	−1·5	+0·2	−1·1
1950–51	1·8 (Dec., Feb., Mar.)	+0·1	−3·1	−0·2	−0·7	−1·2	−0·9
1952–53	1·8 (Dec., Mar., Jan.)	−1·7	−1·8	−1·5	−0·4	−0·5	−0·1

The figures are for Kew Observatory, from the Monthly Weather Report.
* In order of severity.

way in which survival is affected by various features, *e.g.*, lowest temperatures reached, length of periods below particular temperature levels, suddenness or gradualness of onset of cold periods. The shortage of information on these points adds to the difficulty of choosing one out of the various possible ways of assessing severity.

The relative severity of the winters in which our experiments and those of Mansbridge (1936) were done may be estimated by means of the data in the Monthly Weather Report of the Meteorological Office. We have used one of the two sets of figures from Kew Observatory, about 13 miles from Slough. Table III of the Reports gives monthly means of daily minimum temperatures; for each winter, we have picked out the three lowest of these monthly mean minima, and calculated a mean; these final means are shown in the second column of Table I.

Table III of the Report also gives monthly means of daily *mean* temperatures, and shows the amount by which each of these monthly means deviates from an established average for the month, the average being based on records of past years. The deviations are shown in our Table I. The average values shown at the tops of the columns are those used in recent years; the values used in 1934–36 were slightly different and, partly for this reason, the deviations are not precisely comparable with those for 1949–53, but the discrepancies are not great enough to upset the comparison.

Mean temperatures for each month since 1698 are given by Manley (1953), using data from representative stations spread over the greater part of England. We have taken the means for the three coldest months, and combined them in

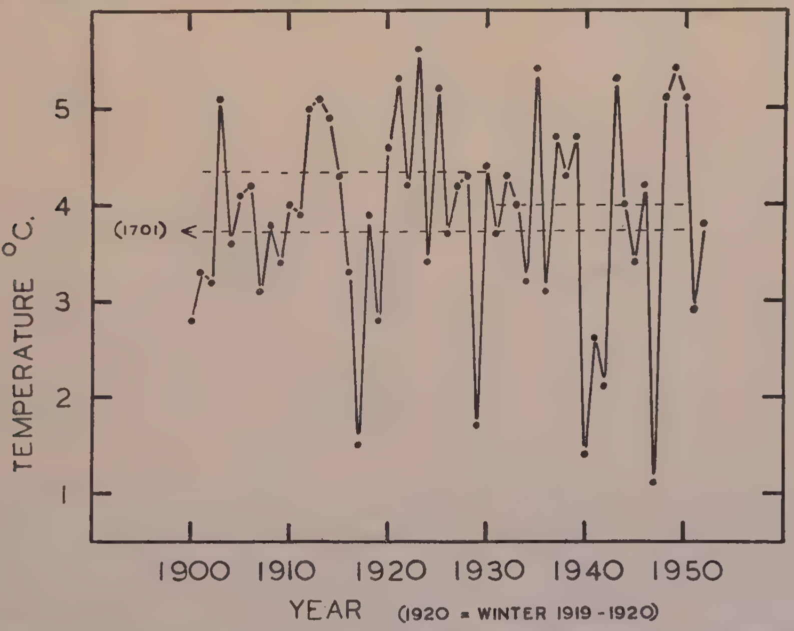


Fig. 1.—Winters in central England. Manley (1953) gives the monthly mean temperature for each month in each year since 1698. For each winter since 1899, the figures for the 3 coldest months have been taken, the mean of the 3 calculated and converted to °C. The winters of 1952–53 and 1953–54, not covered by Manley, would give figures approximating that for 1950–51, to judge from Table I. Manley (*loc. cit.*) also gives means for each of the 12 months over the periods 1701–1950, 1901–30 and 1931–50. His means for December, January and February have been combined, to give the values indicated by the horizontal lines. For a given period, these values are a little higher than means based on the 3 coldest months selected winter by winter.

a single mean, for each winter from 1899–1900 onwards, and plotted them in fig. 1, to show the recent variations in due perspective.

Whereas fig. 1 is based on daily mean temperatures, Table I (second column) is based on daily minima. In Table I the order of severity of the 7 winters concerned is, from mildest to hardest, 1934–35, 1949–50, 1951–52, 1935–36, with 1950–51, 1952–53 and 1953–54 contending for precedence as the most severe. The winter of 1951–52 may be taken as an " average winter " from this point of view. The series gives a fairly good but not complete coverage of the normal range of variation: 1934–35 is the mildest winter in the period since 1923, but in the same period there have been 5 winters colder than any of those above. The most severe has been that of 1946–47 and the next most severe, 1939–40; if included in Table I, these would have the values −0·3°C. and +0·3°C., respectively.

Of course, the meteorological conditions are modified in stores, and in most of our experiments, by the effects of buildings on the movements of temperature; further modification is often imposed by the mass of stored material in which the pests are hiding. These matters are discussed below.

Type of building.

The daily minimum temperatures inside buildings in winter are usually higher than those out-of-doors, the difference depending on the size and composition of the building, its situation, and the bulk of material within. A basis for comparisons is provided by the thermohygrograph charts from various structures in the grounds of the Pest Infestation Laboratory (P.I.L.), Slough, Bucks. Besides those used in overwintering experiments, we shall refer to an additional, more solid building at P.I.L. (the Grain Store), and also to a large warehouse at Brentford, Middlesex. All are listed below.

1. (LS). A small wooden meteorological screen (Pl. XI, fig. 1) containing a thermohygrograph and 10 cultures of insects in 1-lb. jars.
2. A Stevenson meteorological screen (Pl. XI, fig. 2, left). In 1950–51 it contained cultures of insects.
3. A rather heavy imitation of the Stevenson screen, containing cultures (Pl. XI, fig. 2, right).
4. (FH). The Fly Hut (Pl. XI, fig. 3), a flimsy structure of 1 in. pine boards, lined inside with roofing felt against the wood. Corrugated iron roof. No flooring. Some wide cracks at corners at top. Door covered only with flimsy plastic on wire gauze. No bulky contents.
5. (SH). The Summer-house (Pl. XI, fig. 4), a weatherboard shed, roofed with bituminised felting over boards. Walls lined inside with thin metal sheeting. Ceiling of fibre-board. The thermohygrograph stood on the concrete floor, in a position where it caught some afternoon sunlight coming through the glass window. No bulky contents.
6. Hut 49 (Pl. XII, fig. 1), a wooden frame building covered outside and on top with bituminised roofing felt, lined inside the roof and walls with fibre-board, with a concrete floor and numerous windows, of which one was occasionally opened. The building contained a good deal of miscellaneous equipment. A large fibre-board chamber built inside against the N.E. wall contained electric heaters (total 2,800 watts) which were sometimes turned on for a few weeks. The cultures were kept inside cupboards, bins, etc., some heavily lagged.
7. The building used in Mansbridge's experiments (Pl. XII, fig. 2) was a single-brick structure, unheated in the south end where his cultures were kept, while the other end was a culture room maintained at 25°C.
8. (GS). The Grain Store (Pl. XII, fig. 3) has 9-in. brick walls, unlined, asbestos shingle roof, and a ceiling of fibre-board. There is a single window, in the east wall. The floor is of concrete, and about half its area is occupied by grain,

middlings, and other feeding stuffs in sacks or bins. The thermograph element was about 6-in. above the floor.

9. (BW). A large modern 4-storey warehouse, a steel-frame building with brick walls, concrete floors and roof. Each floor above the ground has 2 large lading holes forming part of an open shaft from the ground to the top of the building, and 2 very large openings in the wall, hooded in but open to the dock below. The ground floor is open at each end during working hours. There are numerous glass windows, mostly shut. The situation is beside the Thames at Brentford, surrounded on three sides by river- or dock-water. The thermograph was kept on the first floor, near the south wall.

A direct comparison of temperatures can be made from the charts of thermographs run simultaneously in five of these structures (the ones distinguished above by initial letters). Fig. 2 shows the daily maximum and minimum temperatures in the screen (LS) over 3 successive weeks in February–March 1951. Moving towards the right, the first vertical line (LS) joins the lowest daily minimum to the highest daily maximum for the first week in the screen. The value of the mean of the 7 daily minima and 7 daily maxima is given by the position of the small cross-line. The next line (FH) gives corresponding figures from the Fly Hut. The lines BW and SH refer to the Brentford Warehouse and Summer-house described above. The corresponding lines for the second week appear next to the right, with the addition of a line GS for the Grain Store. Lines for the third week are on the extreme right of the figure.

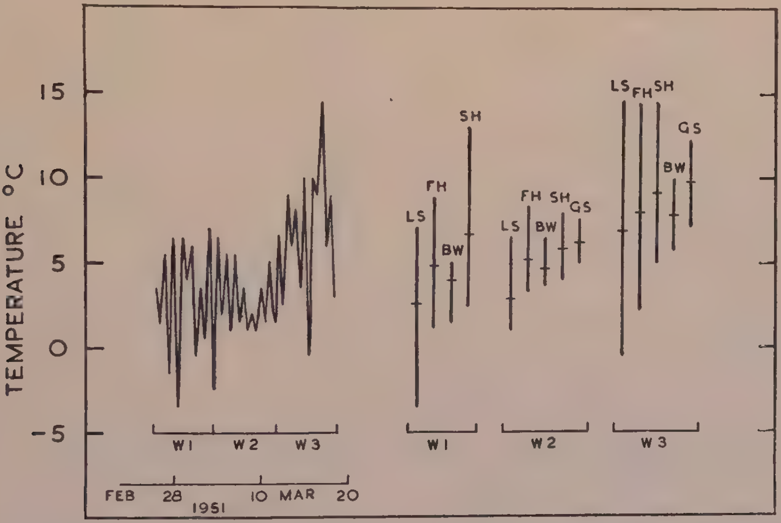


Fig. 2.—Comparison of temperatures in various structures. On the left, daily minimum and maximum temperatures over three successive weeks in a wooden screen. On the right, the vertical lines LS join the highest and lowest temperature in each week, and the small cross-line shows the mean temperature. The other vertical lines give the corresponding data from various buildings described, with the same initial letters, on p. 318, and illustrated (except BW) in Plates XI & XII.

If we take the screen figures as an approximation to official meteorological data, a comparison of the lines for the various buildings with the LS line for the same week will show how the buildings reduced the fluctuations of the temperature. The undiminished range shown by the SH line for the first week is a result of direct sunlight having passed through the window and fallen on the instrument. The effects of sun and of air movement, as modified by the situation and structure of the building, make any detailed interpretation of temperature differences a complex and difficult matter.

Another sort of comparison can be made by working out the mean daily minimum temperature over the three coldest months, as used to compare winters in Table I. By comparing the values for various buildings with those from outdoor screens (and also with figures from the Monthly Weather Report), we arrive at an index of the effect of the building. In the case of Hut 49 there were cupboards or cabinets, etc., also to be taken into account (see p. 325). Table II shows the relative protection given by the various buildings, etc., estimated on this basis. The use of the symbols A and B serves merely to emphasise a difference in degree between severer and milder exposures, the former with minimal protection from the structure holding the cultures.

Further comparative figures are given in Table III.

TABLE II.

Effects of buildings, cupboards, etc., on mean daily minimum temperatures.

Situation, and winter	Mean daily minimum temperature in 3 coldest months °C.	Difference from that of outdoor screen °C.	Difference from that of Kew °C.
B8 Brick Hut (Mansbridge), 1934–35	(7·1?)*	—	(+3·1?)*
B6 Cupboard in Hut 49, 1950–51 (Some effect from heaters)	6·15	+5·45	+4·31
B5 Cabinet in Hut 49, 1952–53	5·83	+4·66	+4·05
B1 Brick Hut (Mansbridge), 1935–36	(5·5?)*	—	(+3·3?)*
B4 Bin in Hut 49, 1950–51	5·24	+4·54	+3·41
B3 Cupboard in Hut 49, 1951–52	5·10	+1·94	+2·58
Brentford warehouse, 1951–52	4·63	—	+2·13
B2 Summer-house, 1949–50	4·57	+1·66	+1·24
Brentford warehouse, 1950–51	3·76	—	+1·96
A4 Screen, 1951–52	3·16	0	+0·64
A3 Fly Hut, 1951–52	2·87	−0·29	+0·35
A2 Fly Hut, 1950–51	1·71	+1·01	−0·13
A0 Screen, 1953–54	1·53	0	−0·27
A1 Screen, 1950–51	0·70	0	−1·20

* A value for the mean minimum in each of Mansbridge's two experiments was estimated approximately by comparing the absolute monthly minima in his graphs with the corresponding ones for Kew, and adding the differences to the corresponding mean minima for Kew, for each of the three coldest months.

Compared with those we have been discussing, heated buildings provide very different conditions. The winter temperatures are much higher than those considered above, and nearly all the common pest species can overwinter in them without difficulty. Of course, the situation may be complicated if part of an establishment is heated, while other parts are only slightly affected by the heating system.

Protection afforded by materials in storage.

The nature of the stored foodstuffs, etc., and the depth to which pests may have penetrated are clearly important factors affecting the temperatures experienced. Oxley (1948, p. 11) points out that daily fluctuations in temperature do not penetrate appreciably below 6 inches into bulk grain, and writes: "In

TABLE III.

Comparison of low temperature conditions in different experiments, ranged in approximate order of severity.

Exposure number	Winter	Situation of cultures and of thermograph	Mean min. temp. (3 months Table II) °C.	Lowest temp. reached (nearest °C.)	No. of days when temp. fell as low as, or lower than, specified levels; and, in brackets, the three longest periods (to nearest 0·5 day) continuously at or below thes elevels						
					−6°C.	−4°C.	−2°C.	0°C.	+2°C.	+4°C.	+6°C.
B10	1953-'54 (24 Dec.–14 Jan.)	Cabinet in Hut 49	—	+3	0	0	0	0	0	**4** (1·5, 0·5)	**15** (5, 0·5, 0·5)
B9	1952 (29 Nov.–15 Dec.)	Cabinet in Hut 49	—	−1	0	0	0	**4** (2)	**10** (3·5, 1, 1)	**11** (10·5)	**14** (11, 1·5)
B8	1934–'35	Brick Hut (Mansbridge)	7·1?	0	0	0	0				
B7	1952–'53 (29 Nov.–12 Jan.)	Cabinet in Hut 49	—	−1	0	0	0	**4** (2)	**10** (3·5, 1, 1)	**12** (10·5)	**23** (11, 3·5, 2·5)
B6	1950–'51	Cupboard in Hut 49*	6·15	−1	0	0	0	**2** (0·5)	**8** (2, 1·5, 0·5)	**21** (4·5, 2·5, 2)	**48** (7·5, 6·5, 2·5)
B5	1952–'53 (29 Nov.–7 Apr.)	Cabinet in Hut 49	5·83	−1	0	0	0	**4** (2)	**12** (3·5, 1, 1)	**21** (10·5, 1·5)	**60** (11, 4·5, 3·5)
B4	1950–'51	Bin in Hut 49	5·24	+2	0	0	0	0	**3** (0·5)	**42** (2, 2, 1)	**111** (7, 5, 4)
Bx	1953–'54 (16 Dec.–8 Feb.)	Cabinet in Hut 49	—	−1	0	0	0	**5** (1, 0·5, 0·5)	**12** (3·5, 2, 1·5)		
B3	1951–'52	Cupboard in Hut 49	5·10	0	0	0	0	**2**	**11** (2, 0·5, 0·5)	**38** (18, 6, 3)	**69** (32, 6, 4·5)
										21 (13, 1·5, 0·5)	**36** (17, 4·5, 1·5)
B2	1949–'50	Summer-house (Pl.XI, fig. 4)	4·57	−1	0	0	0	**7** (0·5, 0·5)	**24** (6, 0·5)	**54** (8·5, 2·5, 1)	**115** (16·5, 3·5, 3·5)
B1	1935–'36	Brick Hut (Mansbridge)	5·5?	−2	0	0		**11** (2)			
A4	1951–'52	Screen (Pl.XI, fig. 2, right)	3·16	−4	0	**2**	**10**	**23** (0·5, 0·5, 0·5)	**51** (1, 1, 0·5)	**94** (2·5, 2·5, 2)	**121** (12·5, 5·5, 3·5)
A3	1951–'52	Fly Hut (Pl.XI, fig.3)	2·87	−5	0	**1**	**11** (0·5)	**23** (0·5, 0·5, 0·5)	**53** (1, 1, 0·5)	**87** (12·5, 5·5, 2·5)	**120** (13, 7, 5·5)
A2	1950–'51	Fly Hut (Pl.XI, fig.3)	1·71	−6	**1**	**5**	**15** (0·5, 0·5, 0·5)	**37** (3, 2, 2)	**89** (9·5, 7, 4·5)	**130** (24·5, 5, 4·5)	**164** (25·5, 8, 7·5)
A1	1950–'51	Screen (Pl.XI, fig. 2, left)	0·70	−5	0	**11**	**28** (0·5, 0·5, 0·5)	**75** (3·5, 3·5, 2·5)	**120** (23·5, 3·5, 3)	**160** (25, 5·5, 4·5)	**174** (25·5, 13·5, 12·5)
A0	1953–'54	Screen (Pl. XI, fig. 2, right)	1·53	−10	**6** (0·5, 0·5)	**11** (0·5, 0·5)	**20** (2·5, 1·5, 1)	**34** (4, 3·5, 1)	**57** (13, 2, 2)	**80** (16, 5, 2·5)	**99** (19, 6, 4·5)

* After mid-December, the temperature was raised by amounts varying up to 4°C., owing to the proximity of electric heaters.

Britain the usual mean temperature range over the year is about 20°F., which is reduced to 1°F. at a depth of about 9 feet."

Dr. J. A. Freeman (unpublished notes) recorded temperatures at Millwall Central Granary in September 1940. Over the period 4th–29th September, the daily mean temperature fell from 75°F. (24°C.) to 50°F. (10°C.) out-of-doors and to 55·5°F. (13°C.) in the free space above a stowage of bulk wheat, while the temperature 3 feet down in the wheat fell from 64° to 61°F. (17·8° to 16·1°C.).

T. A. Oxley & J. P. Heslop (P.I.L., unpublished report) measured the rate of fall of temperature in a large, rather loose stack of maize, in 2·25 cwt. sacks, in a cold store. The initial temperature was just over 9°C. After the cold was turned on, the air temperature fell to 0°C. in 16 days and remained about that level. The temperature 2 feet into the stack (indicated by thermocouples deep in the sacks) was 5·5°C. after 16 days and 2·3°C. after 36 days. At 3·5 feet from the surface it was 6·9° C. after 16 days and 3·7°C. after 36 days.

Bovingdon (1933) measured the temperatures inside a 220-lb. bale of tobacco put into a cold room, and found no appreciable difference from air temperature after about 3 to 5 days. In a hogshead of tobacco there was no appreciable difference after about 16 days. Tenhet & Bare (1951) showed the trends of internal temperatures after cases of cigar tobacco were put into cold storage; after 6 days the temperature at 10 in. depth was within 1°C. of the external temperature, while at 15 and 21 in. the temperature was still about 4°C. higher, but falling sharply.

Considering the above examples from another angle, they illustrate the heat-retaining capacity of stored materials, more particularly those kept in large bulks or stacks. For example, if bulk grain is put into storage at 20°C., the inner parts of the bulk will not fall much below this temperature in the course of the ensuing winter. This is obviously a matter of great importance in relation to questions of overwintering.

Officers of the Infestation Control Division of the Ministry of Agriculture, Fisheries and Food have recorded various examples of the successful overwintering of cold-susceptible species in stacks of materials in which no heating was observed. For example, a few *T. castaneum* survived the winter of 1951–52 in this way in large stacks of decorticated groundnuts in bags, in a warehouse in Hull. Survivals of *R. dominica*, *C. oryzae* and *T. castaneum* have been recorded in unheated stores in the centre of stacks of bagged grain or oilseeds (Dr. J. A. Freeman, *in litt.*).

Heating of the immediate environment.

If there is a local source of heat, cold-susceptible insects may overwinter successfully in the area affected. Freeman (1948*a*) refers to the survival of *T. castaneum* over the winter in the vicinity of hot pipes.

It is well known that stored products in bulk and sometimes in sacks may become hot as a result of the action of micro-organisms, insects or mites. When this happens, part at least of a pest population may escape being exposed to the low winter temperature. In this way, cold-susceptible insects may easily survive the winter. Freeman (1948*a*) refers to the heating of grain, and consequent survival of the winter, by such species as *R. dominica*, *T. castaneum* and *Latheticus oryzae* Waterh., and to a similar survival of *C. cephalonica* and *Ephestia cautella* (Wlk.) in heating groundnuts.

Heating is much less likely to develop in a small or shallow mass of material, because of the relatively high rate of heat loss to the surroundings under such conditions. Moreover, at the low temperatures of winter the metabolic rates of all organisms are so much reduced that a significant amount of heating seems unlikely to occur. Hence heating is most likely to develop in the deeper parts of bulks or tight stacks, provided they have been put into store under warmer conditions, and provided they are sufficiently infested, or damp. That is to say, the sites where heating is most likely are some of those which in any case provide some refuge from the cold, even without heating.

In our experiments, it seemed unlikely that any appreciable heating could begin at the low winter temperatures in the experimental sites, and in the small masses of material used. A few checks were made by leaving thermometers with the bulbs buried in the culture material in some of the 2-lb. jars. The cultures were of *A. fasciculatus*, *C. oryzae*, *L. minutus*, *T. confusum*, *Dermestes maculatus* Deg., *R. dominica* and *Lasioderma serricorne* (F.). The temperatures, read off in three successive weeks after the cultures had been *in situ* for 6–9 weeks, were all within 1° of 6·5°C., and showed there was no significant heating.

SYSTEMATIC LIST OF SPECIES.

In Table IV and in the Detailed Comments (pp. 331–344) on the results, the species are arranged alphabetically. They are listed below in systematic order, following that given by Kloet & Hincks (1945). The three species marked "[M. only]" were included in experiments by Mansbridge (1936), but not in our tests.

Thysanura
LEPISMATIDAE
Lepisma saccharina L.—Silverfish

Orthoptera
BLATTIDAE
Blatta orientalis L.—Common Cockroach
Periplaneta americana (L.)—American Cockroach

Lepidoptera
PHYCITIDAE
Plodia interpunctella (Hb.)—Indian Meal Moth
Ephestia kuehniella Zell.—Mediterranean Flour Moth, Mill Moth
Ephestia elutella (Hb.)—Cacao Moth, Tobacco Moth
Ephestia cautella (Wlk.)—Dried-currant Moth
GALLERIIDAE
Achroia grisella (F.)—Lesser Wax Moth
Corcyra cephalonica (Stnt.) [M. only]—Rice Moth
Galleria mellonella (L.)—Wax Moth
GELECHIIDAE
Sitotroga cerealella (Ol.)—Angoumois Grain Moth
OECOPHORIDAE
Hofmannophila pseudospretella (Stnt.) [M. only]—Brown House Moth
TINEIDAE
Trichophaga tapetzella (L.)—Tapestry Moth, Carpet Moth
Tineola bisselliella (Humm.)—Clothes Moth
Tinea granella (L.)—Corn Moth
Tinea spp. (casebearers)
(*T. pellionella* (L.) and *T. columbariella* Wocke)

Coleoptera
CLERIDAE
Necrobia rufipes (Deg.)—Copra Beetle
DERMESTIDAE
Dermestes maculatus Deg. (= *D. vulpinus* F.)—Leather Beetle
Dermestes frischii Kug.—Hide Beetle

- **Coleoptera**—*continued*
  - DERMESTIDAE—*continued*
    - *Dermestes lardarius* L.—Bacon Beetle
    - *Anthrenocerus australis* (Hope)—Australian Carpet Beetle
    - *Attagenus megatoma* (F.) (= *A. piceus* (Ol.)) Black Carpet Beetle
    - *Attagenus pellio* (L.)—Fur Beetle
    - *Trogoderma granarium* Everts—Khapra Beetle
    - *Trogoderma versicolor* (Creutz.)—Larger Cabinet Beetle
    - *Anthrenus vorax* Waterh.—Furniture Carpet Beetle
    - *Anthrenus verbasci* (L.)—Varied Carpet Beetle
  - TROGOSITIDAE
    - *Tenebroides mauritanicus* (L.)—Cadelle
  - NITIDULIDAE
    - *Carpophilus hemipterus* (L.)—Dried-fruit Beetle
    - *Carpophilus dimidiatus* (F.)—Corn Sap Beetle
    - *Carpophilus ligneus* Murray
  - CUCUJIDAE
    - *Ahasverus advena* (Waltl)—Foreign Grain Beetle
    - *Oryzaephilus surinamensis* (L.)—Saw-toothed Grain Beetle
    - *Oryzaephilus mercator* (Fauv.)—Merchant Grain Beetle
    - *Laemophloeus minutus* (Ol.)—Flat Grain Beetle
    - *Laemophloeus ferrugineus* (Steph.)—Red Rust Grain Beetle
    - *Laemophloeus turcicus* Grouv.
    - *Laemophloeus pusilloides* Steel & Howe
  - BOSTRYCHIDAE
    - *Rhizopertha dominica* (F.)—Lesser Grain Borer
  - ANOBIIDAE
    - *Stegobium paniceum* (L.)—Biscuit Beetle
    - *Lasioderma serricorne* (F.)—Cigarette Beetle
    - *Dorcatoma bibliophagum* Magalh.
  - PTINIDAE
    - *Gibbium psylloides* (Czenp.)—Hump Spider Beetle
    - *Stethomezium squamosum* Hinton—African Spider Beetle
    - *Mezium affine* Boield.
    - *Trigonogenius globulus* Sol.—Globular Spider Beetle
    - *Niptus hololeucus* (Fald.)—Golden Spider Beetle
    - *Pseudeurostus hilleri* (Rter.)—Japanese Spider Beetle
    - *Ptinus fur* (L.)—White-marked Spider Beetle
    - *Ptinus tectus* Boield.—Australian Spider Beetle
    - *Ptinus sexpunctatus* Panz.
  - TENEBRIONIDAE
    - *Gnathocerus cornutus* (F.)—Broad-horned Flour Beetle
    - *Gnathocerus maxillosus* (F.)
    - *Tribolium castaneum* (Hbst.)—Rust-red Flour Beetle
    - *Tribolium confusum* Duv.—Confused Flour Beetle
    - *Tribolium destructor* Uytt.—Dark Flour Beetle
    - *Latheticus oryzae* Waterh.—Long-headed Flour Beetle
    - *Palorus ratzeburgi* (Wissm.)—Small-eyed Flour Beetle
    - *Palorus subdepressus* (Woll.)—Depressed Flour Beetle
    - *Alphitobius diaperinus* (Panz.)—Lesser Mealworm
    - *Alphitobius laevigatus* (F.) (= *A. piceus* (Ol.))—Black Fungus Beetle
    - *Tenebrio molitor* L.—Yellow Mealworm
    - *Tenebrio obscurus* F.—Dark Mealworm

Coleoptera—*continued*

BRUCHIDAE

Acanthoscelides obtectus (Say)—American Seed Beetle
Callosobruchus chinensis (L.)—Cowpea Beetle
Callosobruchus analis (F.)
Caryedon fuscus (Goeze)—Groundnut Beetle

ANTHRIBIDAE

Araecerus fasciculatus (Deg.)—Cacao Weevil

CURCULIONIDAE

Caulophilus latinasus (Say) [M. only]—Broad-nosed Grain Weevil
Calandra granaria (L.)—Grain Weevil
Calandra oryzae (L.)—Rice Weevil

Methods and Procedure.

The general procedure was to expose cultures of insects to winter conditions in various situations, and to observe them *in situ* at monthly intervals, with a thorough examination at the end of the experiment. Continuous records of the temperature and humidity were kept by means of thermohygrographs.

Preparation of the insects.

New cultures were set up of insects normally kept in the insectaries: the appropriate foodstuffs (listed with Table IV) were put into 7-lb. or 2-lb. glass jam jars to a depth of 5 to 8 cm., adult insects were introduced, and the jars kept in a controlled room at 25°C., 70 per cent. relative humidity for about 7 days, or sometimes about 14 days. This ensured that the food was moisture-conditioned and that eggs were present. About 2 hours before transferring the jars to the experimental conditions, larvae were added, and in some cases also pupae. The transfer to the colder conditions was always made on a relatively mild day.

Exposure of the insects.

The meteorological screens and various buildings in which the cultures were exposed in one or other of the experiments have been described on p. 318. The cultures exposed in Hut 49 were further protected by cupboards etc., as follows:—

Bx, B5, B7, B9 and B10: in a Hearson incubator cabinet, with extra lagging of cotton-wool and paper, but no heaters.

B6: in a closed wooden cupboard, chiefly of 3-ply, lagged above and at the sides with a loose sheet of soft fibreboard.

B4: in a large metal bin, closed above with a number of layers of balloon fabric. In this instance the thermograph was not with the cultures, but in an adjacent metal tank closed above with a sheet of hard asbestos board.

B3: in a wooden cupboard lagged above and below and on 3 sides by piles of cardboard forming solid walls about a foot thick.

While the majority of the experiments extended over the whole winter (early November to at least the end of April), B5 lasted a little over 4 months, Bx lasted only 8 weeks, B7, 6 weeks, B10, 3 weeks, and B9 only 16 days.

Observation of the insects.

Observations were made on the cultures at approximately monthly intervals throughout the winter, but the food was not shaken or disturbed. Since larvae burrowed into the food, it was usually impossible, except in the case of the Anobiids and Ptinids which formed cocoons against the side of the jar, to see what stage they had reached. Adults, however, were generally on the food surface and it was possible to tell from their appearance whether they were still alive. In cases of doubt, torpid insects could be revived by the warmth of the hand.

It was not possible to examine the cultures in detail immediately after the experiments finished in April. The experiments carried out in 1949–50–51 were left in the experimental situations and examined between June and October. The 1951–52 experiments were transferred on June 9th to a room kept at 25°C., 70 per cent. relative humidity, and examined during the ensuing four weeks.

For the final examinations, all insects were carefully sorted out of the food by hand and the numbers alive and dead were counted. Those that appeared dead were kept in the controlled room for a fortnight to see if any would recover, and in some cases the culture was returned to the room to show whether anything would breed through.

Recording of temperature and humidity.

In each site used for the exposure of cultures, a thermohygrograph was kept, together with a maximum and minimum thermometer or at least one ordinary thermometer. Besides setting the temperature pen at the correct line on the chart, it was found necessary to adjust the calibration of some of the instruments, to ensure that the pen still indicated correctly at lower and higher temperatures. Occasional accidents occurred, such as the stopping of the clock in the drum or a pen losing contact with the chart. The resulting gaps were made good by graphing the records from several places, over a fairly long period, on a common graph sheet, so that the missing parts could be drawn in by comparison with the other records. By such measures, and by adherence to a strict routine including many minor precautions, fairly reliable records were secured.

Less detailed attention was given to the humidity records, but every few weeks, when not weekly, the hair elements were thoroughly wetted with distilled water, and the pens set on the 95 per cent. line.

Comparison of different exposures.

Two sources of data have been used in the comparative study of the runs of temperature in these experiments. The first is the Monthly Weather Report, which gives absolute and mean maximum and minimum temperatures for each month at numerous meteorological stations in Britain. The second and chief source is our thermograph charts, which provide a more or less complete record of the temperatures from hour to hour throughout the experimental periods. The data have been used in the following ways:—

1. In Table I, the winters covered by our experiments and Mansbridge's have been compared using the monthly means of daily minimum and daily mean temperatures taken from the Monthly Weather Report.
2. Using monthly means calculated from the daily minima in our records, we have similarly compared the different exposures in our experiments (Table II). This provides a basis for estimating the effects of different buildings, etc., in modifying the temperature. It also enables us to list the experimental exposures in order of severity (by this criterion), which is useful in the general interpretation of the biological results.
3. If we knew the modes of reaction of the different species of insects to cold, and if we knew these to be substantially the same, some such simple index of the severity of the treatments might be sufficient. But the modes of reaction are mainly unknown and probably differ a great deal as between species. Hence it is necessary to give a fuller account of the temperature conditions. This might be done in many ways, according to what information is thought to be the most relevant to overwintering. Table III represents an attempt at such a summary, but, as already mentioned, where a number of species are involved there is a considerable element of guesswork in choosing the method. It may be

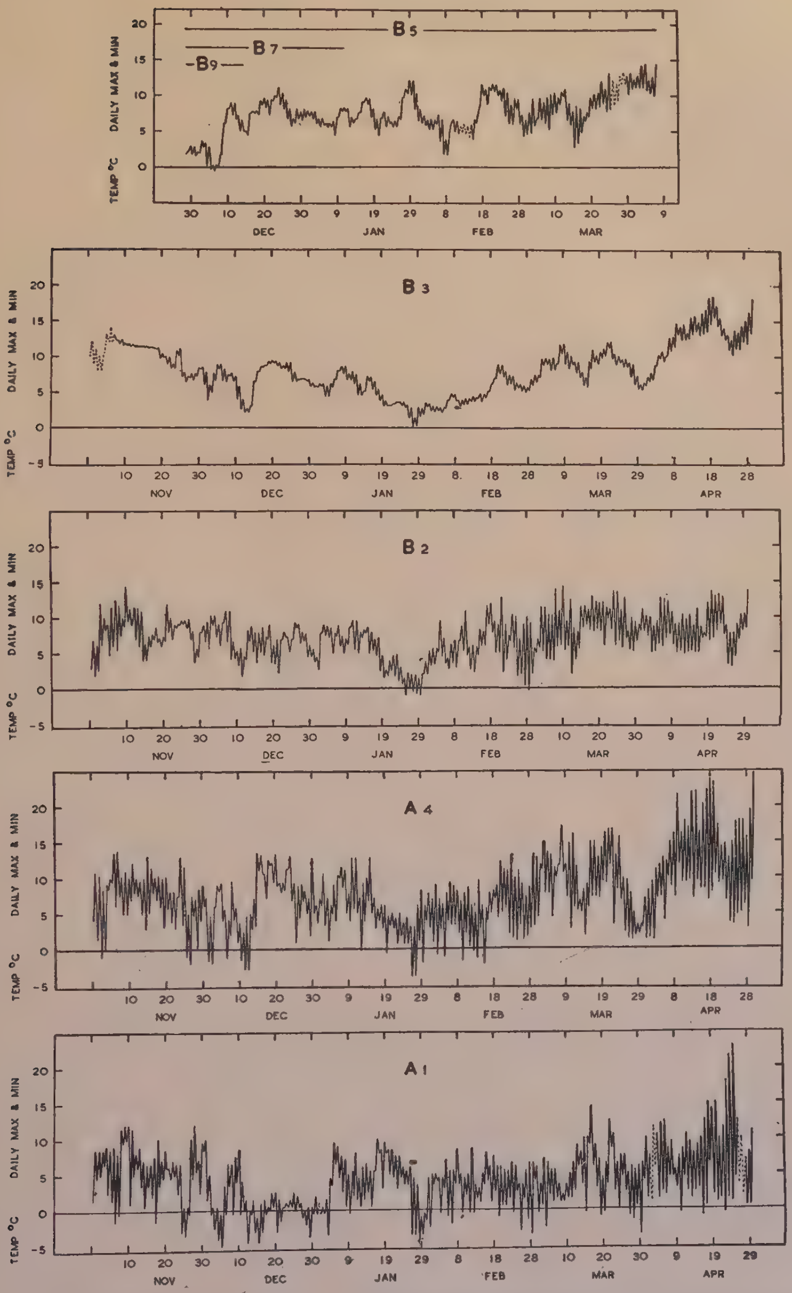


Fig. 3.—Graphs of the daily minimum and maximum temperatures in various experiments.
B9, B7 and B5: In cabinet in Hut 49, 1952–53 (Pl. XI, fig. 5).
B3: In cupboard in Hut 49, 1951–52 (Pl. XI, fig. 5).
B2: In Summer-house, 1949–50 (Pl. XI, fig. 4).
A4: In outdoor screen, 1951–52 (Pl. XI, fig. 2, right).
A1: In outdoor screen, 1950–51 (Pl. XI, fig. 2, left).

Results of overwintering experiments by present authors and some by

(1) Species	(2) Tests (Severe) A0	A1	A2	A3	A4	*B1*	B2	B3	B4	B5	B6	B7	(Mild) *B8*	B9	B10	(3) Number of tests
Acanthoscelides obtectus ..						F	F		F		F					3+1*M*
Achroia grisella						S	S						S			1+2*M*
Ahasverus advena†						F										1*M*
Alphitobius diaperinus ..							F	F								2
,, *laevigatus* ..							F		F		F				F	4
Anthrenocerus australis ..	S			S	S			S								4
Anthrenus verbasci		S	S			S	S									3+1*M*
,, *vorax* ..		S	F				S		S		F					5
Araecerus fasciculatus ..						F	F		F	F	F	F	F	S		6+2*M*
Attagenus megatoma (=*A. piceus*)	S		S		S		S									4
,, *pellio*	S			S	S											3
Blatta orientalis				F	F		S	S								4
Calandra granaria			F			F	F		F	F		F	S	S		6+2*M*
,, *oryzae* ..						F	F		F	F		F	F	F	S	6+2*M*
Callosobruchus analis ..								F								1
,, *chinensis* ..									F		F					2
Carpophilus dimidiatus ..						F	F		F		F		F		F	4+2*M*
,, *hemipterus* ..							F				F					2
,, *ligneus* ..							F									1
Caryedon fuscus							F	F	F		S					4
Caulophilus latinasus† ..						F							F			2*M*
Dermestes frischii	S			S	S				S							4
,, *lardarius* ..		S	S			S	S						S			3+2*M*
,, *maculatus* (=*D. vulpinus*) ..						F	F		F	F	F	F	F	F	S	7+2*M*
Dorcatoma bibliophagum ..				F	F			F								3
Ephestia cautella			F			F			F		F		S			3+2*M*
,, *elutella* ..		F	S			S	S						S			3+2*M*
,, *kuehniella* ..		S	S			S	S						S			3+2*M*
Galleria mellonella	S			S			S									3
Gibbium psylloides	S				S	S	S						S			3+2*M*
Gnathocerus cornutus ..						F	F		F		F		F		F	4+2*M*
,, *maxillosus* ..															F	1
Hofmannophila pseudospretella† ..						S										1*M*
Laemophloeus ferrugineus ..	S			S				S								3
,, *minutus* ..							F		F	F		F		F		5
,, *pusilloides* ..							F		F	F		F		F		5
,, *turcicus* ..		F	S			S	S						S			3+2*M*
Lasioderma serricorne ..						F	F			F		F		S	S	5+1*M*
Latheticus oryzae				F				F							S	3
Lepisma saccharina ..		S					S									2
Mezium affine		S					S									2
Necrobia rufipes	F														S	2
Niptus hololeucus		S	S			S	S									3+1*M*
Oryzaephilus mercator ..			F			F	F		F	F	F	F		F	F	8+1*M*
,, *surinamensis*	S		S		S	F	S		S		S					6+1*M*
Palorus ratzeburgi							F		F		F				S	4
,, *subdepressus* ..							F		F							2
Periplaneta americana ..								F								1
Plodia interpunctella ..	S		S			S	S		S		S		S			5+2*M*
Pseudeurostus hilleri ..		S					S									2
Ptinus fur		S					F									2
,, *sexpunctatus* ..		S					S									2
,, *tectus*		S				S	S						S			2+2*M*
Rhizopertha dominica ..						F	F		F	F	F	F		S	S	7+1*M*
Sitotroga cerealella		F	F	S	S	F	S									5+1*M*
Stegobium paniceum ..	S				S	F	S						S			3+2*M*
Stethomezium squamosum ..		F					S									2
Tenebrio molitor		S				S	S						S			2+2*M*
,, *obscurus* ..	S				S	S	S						S			3+2*M*
Tenebroides mauritanicus ..					S	S							S			1+2*M*
Tinea spp. (casebearers)* ..	S		S	S	S		S									5
Tinea granella				S												1
Tineola bisselliella		S	S			S	S						S			3+2*M*
Tribolium castaneum ..						F	F		F	F	F	F	F	F	S	7+2*M*
,, *confusum* ..						F	F		F	F	F	F	F	S		6+2*M*
,, *destructor* ..				F				F							S	3
Trichophaga tapetzella ..	S			S												3
Trigonogenius globulus ..		S					S									2
Trogoderma granarium ..	S	S				S	S						S			3+2*M*
,, *versicolor* .		S	S			S	S						S			3+2*M*

‡ For n

Mansbridge (1936; entries referring exclusively to his work are italicised).

(4) Stages and approx. numbers used in each test	(5) Food No.	(6) In tests with some survivals		(7) In tests with no survivals
		Stages shown able to survive	Stages shown not to survive	Stages shown not to survive
E, 50L, 50A	17			E, L, A
E, L, P, A	21	L	A	
500, *L*, *A*	2			*L*, *A*
E, 70L, 60A	1,2			E, L, A
E, 80L, 10P, 80A	1,2			E. L, P, A, (No pupae in B10)
100L	9	L (+)		
60L	9	L (+)		
E, 100L, 20P, 100A	9	L (−) to (±)	A?	L, A, (P in A2)
100 E, L, P, A	11	(−)	E	E, L, P, A
E, 100L, 100A (9A in A0)	6	L(+); A(+) in A4	A in A0, A2 & B2	
E, 20L, 20A	6	?E(+), L(+); A(±) in A4, A(+) in AO	A in A3	
10 large nymphs	5	B4: nymph (±) B2: nymph (±) died in May		
E, 200L, 100A	13	A(+)		E, L, A
E, 200L, 100A	13	A(±)		E, L, A
E, 50L, 50A	16			E, L, A
E, 50L, 50A	16			E, L, A
E, 100L, 100A (4 in B10)	10			E, L, A
E, 100L, 100A	18, 19			E, L, A
E, 100L, 100A	18, 19			E, L, A
E, 50L, 50A	20		A	E, L, A
100A	?			A
30L, 20A	8	L (±); A(−) to (+)	A in A0	
E, 60L, 50A	8	L, A		
E, 100L, P, 100A	8	L(+) A(+)		E, L, P, A
100L	4			L
E, 50L, 50P, 25A	3	?L		
E, 50L, 40P, 40A	3	L(+), ? P(+)	A	L, P, A
E, 100L, 100P, 25A	3	L(+), P(+) in B2	A	
A4 and A0: 50L B2: 200, E, L, P, A	21	L; L(−) in A0	A	
200, E, L, P, A	7	*L*(+) (? in A0), A0 (+) in A0		
E, 100L, 70A (20 in B10)	4			E, L, A
E, 200L, 30A	4			E, L, A
100*L*	?	*L*		
E, 100L, 100A	5	? L(+), A(+) in A0	A in A3	
E, 200L, 125A	5			E, L, A
E, 200L, 125A	5			E, L, A
E, 200L, 125A	5	L(+), A(+)		E, L, A
E, 200L, 100A	4	L(−) in B9; A(±) and L(+) in B10	A in B9	E, L, A
E, 60L, 30A	15	L(±) in B10	A in B10	E, L, A
A1:6, B2:50	5	(+)		
200L	7	L(+)		
E, 50L, 10A	8+20	L(+)	A	E, L, A (1 moribund larva)
E, L, P, A	7	L(+), ?A(+)		
E, 100L, 200A	5			E, L, A
E, 100L, 200A	5	?L(±), ?A(−)		*L*, *A*
E, 100L, 100A (E, 10A in B10)	4	A(±) in B10		E, L, A
E, 100L, 100A	2			E, L, A
6 nymphs, 3A	5			? (too few)
E, 60L, 100P, 30A	3	L(−) to (+)	P, A	
200, E, L, P, A	7	(+)		
200, E, L, P, A	7			Discounted
200, E, L, P, A	7	B2:L(+), A(+)		
A1:200, E, L, A	7	A1:(+)		
E, 200L, 100A	13	A(+) and L(+) in B10		E, L, A
E, 100L, 70A	13			E, L, A
E, 100L, 100A	4	L(+), ?A(±)		*L*, *A*
200, E, L, A	7	A(±)	E	E, L, A
E, 60L, 40A	5	L(+)		
60L	5	L(+)		
14L, 12A	12	L(+), A(+)		
100L, 100A	9	L(+)		
40L (?E, P)	13			
E, 100L, 100A	9	L(+)		
E, 100L, 20P, 80A	1	L(−)		E, L, P, A
E, 100L, 20P, 80A	1	L(−)		E, L, P, A
E, 100L, 50A	4	A (+) Some moribund larvae		E, L, A
E, 30L, 15A	9	L(+)	A	
200, E, L. P A	7	A1:(±).B2:L(+)		
100*L*; + 60A in A0	14	L(+);L(+) & A(−) in A0		
E, 100L, 100A	5	L(± to +)	E, A	

ee p. 330.

noted that the order of severity indicated by the method of Table III is nearly the same as that based on means of daily minima in Table II.

4. Finally, fig. 3 shows graphs of some of the runs of temperature in the experiments. Here the only simplification is that instead of the natural curve with all its minor irregularities we have plotted only the early-morning minimum and the afternoon maximum temperature for each day, and joined these points by straight lines. On occasions when the temperature did not conform to this typical diurnal cycle it was still found possible to represent the trend of the changes by plotting a pair of points for each day.

Results.

The results are set out in a somewhat condensed form in Table IV. The notes in the legend explain the entries. In brief, column (2) shows under which conditions (as listed in Table III) various species completely failed to survive the winter (F) and under which conditions there were some survivors (S). It should be noted that exposures B7, B10 and B9 were much shorter than the others, only 6 weeks, 3 weeks, and 16 days respectively. One exposure, Bx, is not included in Table IV.

Columns (6) and (7) list such inferences as could be safely drawn from the observed results. The experiments were designed to test whether or not populations could survive, rather than to test the resistance of the different stages. Much fuller information on the latter point could be gained by keeping the different stages in separate containers, but there would still be difficulties of interpretation owing to the possibility of insects passing from one developmental stage to the next during the course of the experiments. Eggs or other normally short stages can hardly be taken as having overwintered unless it can be shown that they have remained in that stage throughout the cold period; furthermore, although an experiment may begin with eggs, along with other stages, and although eggs may be observed monthly throughout the winter it does not follow that they are the same ones—in fact, the eggs as such may be escaping the cold by hatching after a period; such points were considered in making the

---

Column (2): The symbols A0 to B10 refer to the sets of conditions outlined in Table III. For each test in which a species was included, the symbols S and F show whether there were some survivals (S), or none (F).

Column (3): The numbers followed by *M* refer to Mansbridge's experiments; *e.g.*, $4 + 2M$ means 4 trials by the present authors and 2 by Mansbridge.

Column (4): The numbers are those used in each of our experiments, except in a few cases where they refer to Mansbridge's, as indicated by (*M*).
E = eggs, L = larvae, P = pupae, A = adults.

Column (5): The numbers refer to the various food materials used, as follows:—
1, Toppings; 2, toppings over a wet pad; 3, toppings and glycerine; 4, toppings and dried yeast powder; 5, toppings, rolled oats and dried yeast powder; 6, toppings, rolled oats, dried yeast powder and flannel; 7, toppings and fishmeal; 8, fishmeal and dried yeast powder; 9, fishmeal, dried yeast powder and flannel; 10, rolled oats and dried yeast powder; 11, maize; 12, maize and rolled oats; 13, wheat; 14, wheat and rolled oats; 15, wholemeal flour and dried yeast powder; 16, lentils; 17, kidney-beans; 18, uncooked dates and figs, with dried yeast powder; 19, boiled dates and figs, with dried yeast powder; 20, groundnuts; 21, brood-comb.

Columns (6) and (7): Symbols for life-history stages as in column (4). These columns show which stages survived the whole periods of the tests, or failed to survive, as far as this could be inferred from the observations made. A few slightly doubtful inferences are included and queried; substantially doubtful or inconclusive results have been omitted.

Wherever the information is available, signs are added to show whether the proportion of the hardy stage surviving is over 25% (+), under 5% (−), or between 5% and 25% (±).

† Species tested by Mansbridge only.

* A mixed stock of *Tinea columbariella* Wocke and *T. pellionella* (L.), two species of similar appearance and habits (*cf.* Woodroffe, 1950).

entries in columns (6) and (7). No account was taken of the fact that some adults, especially those of some of the moths, are so short-lived that they could not be expected to survive the long periods of these experiments, even if the cold conditions did them no harm. The question we have held primarily in mind in this work is: Can this species, or stage, survive the winter under those conditions? Any evidence throwing light on possible reasons for survival or failure has been noted with interest, but the experiments were not designed to collect it.

Detailed Comments on Results.

Acanthoscelides obtectus.

This Bruchid is adapted to warm climates, and did not survive in our experiments. It was not tested in B7–10. Mathlein (1944) reported that all developmental stages were killed in 6–7 weeks at 0°, or 4 weeks at −2°C., and that an infestation failed to overwinter in a cellar where the temperature was usually about 5° and never below 2°C.

Achroia grisella.

The larvae of the Lesser Wax Moth are probably hardy, but were not tested under the most severe conditions. Although it is distributed throughout the Old World (Corbet & Tams, 1943), it may presumably survive the winter in bee-hives without necessarily being able to withstand the outside temperatures.

Ahasverus advena.

This grain beetle died in Mansbridge's single experiment with it (B1), and in our Bx (Table III). However, Donisthorpe (1939) found large numbers at the bottom of a hay-stack, and the same observation has been made several times by our colleague Mr. G. E. Woodroffe (and *cf.* Jennings, 1932). This suggests it may be cold-hardy, but on the other hand it may overwinter in virtue of warm conditions under the stacks.

Alphitobius diaperinus.

Mallis (1945) describes this as a minor and cosmopolitan household pest. O'Farrell & Butler (1948) listed it among the species surviving only in heated buildings in N. Ireland. It failed to survive in the two experiments made with it, under fairly mild conditions. However, those cultures which were provided with the excess moisture normally required by this species became mouldy before the end of the experiment, and the other cultures may well have been too dry. O'Mahony (1950) found *A. diaperinus* in very large numbers on waste ground near the Dublin docks, sufficiently widespread to suggest a population of long standing.

Alphitobius laevigatus.

The Black Fungus Beetle is commonly imported from hot areas (Howe & Burges, 1952*b*), and in our experiments it failed even in B10. However, as with *A. diaperinus*, the moist cultures became mouldy and the others were probably too dry. *A. laevigatus* has been found out-of-doors in various situations, including fungi in Windsor Forest (Allen, 1948; Verdcourt, 1948), which suggests it is probably established and able to overwinter independently of heated buildings.

Anthrenocerus australis.

The Australian Carpet Beetle is found as a pest in textile mills in Britain and has recently appeared in Holland (Meeuse, 1950), but so far has not been recorded from any but heated premises. Nevertheless, it is clear from our results that the larvae are cold-hardy, so that it may become established here along with

Anthrenus spp. Possibly it requires warmer conditions for the completion of its life-cycle than our summers generally provide (*cf.* the note on *Anthrenus vorax*).

Anthrenus verbasci.

Zacher (1939) lists the Varied Carpet Beetle as native to Germany. It is well established in parts of Britain and is a common inhabitant of certain birds' nests (*cf.* Woodroffe & Southgate, 1951; Woodroffe, 1953). In our experiments with larvae, they readily survived in the most rigorous conditions tested.

Anthrenus vorax.

This Carpet Beetle comes from warm countries. According to Harrison (1944), the optimum conditions for its development are about 32° to 35°C., and cold torpor sets in at the relatively high temperature of 14°C. Nevertheless, Herfs (from Hinton, 1945) records that adults and larvae survive long winter periods when day temperatures are −2° to +2°C. Back & Cotton (1926*c*) wrote that larvae survived about 50 days at −1·1° to +1·7°C., or −3·9° to −1·1°C., that it took 34 days to kill them at −6·7° to −3·9°C., and that they survived 2 days and adults 4 days, at −12·2° to −9·4°C. Our insects seemed to be less hardy than theirs,* but some larvae, at least, survived in three of our experiments, including a few in A1. Thus *A. vorax* is certainly capable of overwintering in Britain and presumably could become established here as a resident pest. It may be that British summer conditions are a barrier to its establishment, for as Hinton (1945, p. 344) emphasises, the pupa needs a temperature not much below 25°C. for its development, pupal mortality being very high at 20°C. (Herfs, 1936).

Attagenus megatoma (= *A. piceus*).

This nearly cosmopolitan Carpet Beetle was first recorded in Britain in 1868 and is now established here (Hinton, 1943*b*). Zacher (1939) lists it as well as *A. pellio* among the species native to Germany. Our experiments show that larvae and adults are able to overwinter in Britain. It is known to survive out-of-doors, sometimes in birds' nests (Hinton, 1945, p. 318). Back & Cotton (1926*c*) recorded its survival for 314 days at −1·1° to +1·7°C., and for 198 days at −3·9° to −1·1°C.

Attagenus pellio.

The Fur Beetle is well established in unheated buildings in Britain (*cf.* O'Farrell & Butler, 1948; Coombs, 1955), and occurs frequently in birds' nests (Hinton, 1945, p. 308; Woodroffe, 1953); it is regarded as a native species (Hinton, 1943*b*). In our experiments, a number of larvae and probably some eggs overwintered in A4, adults in A3 and A0.

Blatta orientalis.

In A4 the last of 10 individuals died before 21st March, in A3 between this date and 19th May, in B2 in May or June. In B3 one was still alive in June. These results suggest that the mortality may have been due not entirely to cold, but also to other causes, such as lack of sufficient moisture. In any case, the results show this species is not to be classed as highly susceptible to cold. It is known to occur out-of-doors in Britain (Gardner, 1954). Mellanby (1939) found that adults taken from 30°C. were killed by 1 hour at −5·5°C., and those from 15°C. by 10 hours at −8°C.

---

* Some such differences should perhaps be expected in a species notable for its variations in colour pattern. Hinton (1945) recognises four pattern varieties.

Calandra granaria.

The Grain Weevil is known to overwinter at times in unheated buildings. Freeman (1948*a*) stated that adults generally survived the winter. O'Farrell & Butler (1948) wrote: " *C. granaria* was seldom introduced into Northern Ireland during 1943 and 1944, except in very small numbers, but during this period, a considerable population was able to maintain itself in the unheated granaries of some of the flour-mills, living in accumulations of grain spillage which were kept warm during the winter by the activity of various species of insects ". It is therefore surprising to find that *C. granaria* completely failed in our experiments, except in the very brief B9. They also failed in one of Mansbridge's experiments, and survived in the mild B8. Various authors have given figures for the maximum survival periods of *C. granaria* on grain at low temperatures, and these are set out in fig. 4. It will be seen that the results of Back & Cotton (1924), Andersen (1938) and Mathlein (1938) fall roughly about a curve. Of special interest are the results of Ushatinskaya (1950*b*), showing the great importance of the humidity conditions (grain moisture content). We have tested the cold-resistance of our

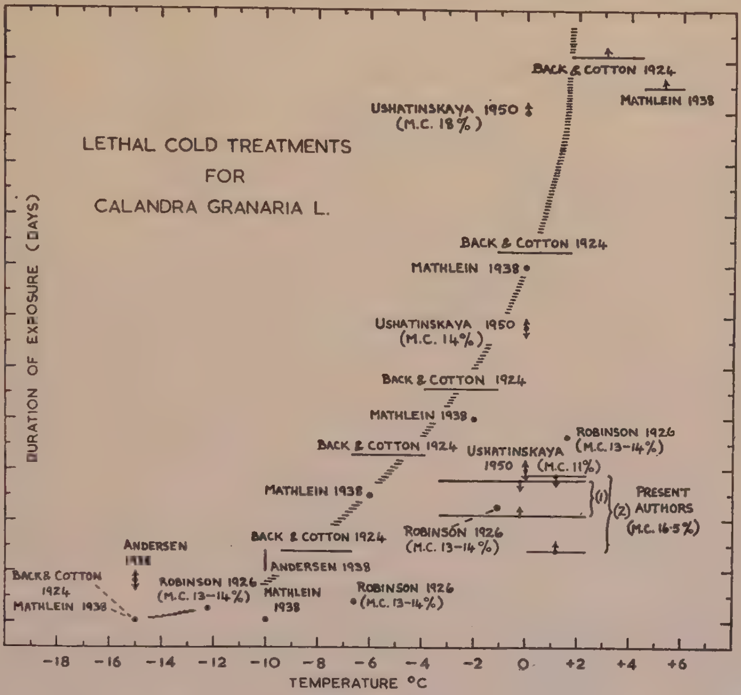


Fig. 4.—Data of various authors for the lengths of exposure required to give complete kill of adults (hardiest stage) of *Calandra granaria.*

When a definite temperature and time has been specified, a dot is drawn. A range of temperature but a single time value is shown by a horizontal line, a single temperature but a range of times is shown by a vertical line. When a time value is specified as an approximation, arrows are shown above and below the dot. A single arrow is used when the time specified is more or less than enough to give complete mortality.

For our own results, from two experiments, the range of temperature variation in each experiment is shown by the horizontal span of a pair of lines, and the mean temperature by a dot on each line. The minimum time value for 100 per cent. mortality lies somewhere between the two lines of a pair.

The diagram shows that the beetles tested by Robinson (1926) were much less resistant than those tested by other authors, whose results fall roughly about a curve, while our own stock (considering the favourably high moisture content of the grain) was even less resistant.

insectary stock by putting small cultures in a refrigerator for various periods. The results are included in fig. 4, and show clearly that our stock is particularly susceptible to cold.

Calandra oryzae.

The Rice Weevil, although primarily an inhabitant of warm countries, is considered to be able to survive mild winters in unheated buildings in southern England (Freeman & Turtle, 1947; Freeman, 1948*a*). For example, it survived the mild winters of 1948 and 1949–50 in sacks of barley stacked in corrugated iron huts at an airfield in Lincolnshire (Dr. J. A. Freeman, *in litt.*). O'Farrell & Butler (1948) wrote that it did not overwinter in N. Ireland in unheated buildings except in warm grain or in heated accumulations of grain spillage in unswept corners in the granaries of some flour-mills. None survived in Mansbridge's experiments nor in any of ours except B10. It may be that, as with *C. granaria*, our insectary stocks are unusually susceptible to cold.

The experimental data listed below show the degree of resistance of *C. oryzae* to various constant low temperatures. There is a discrepancy between Ushatinskaya (1950*a*), who found the eggs to be easily the most resistant stage at temperatures of −5° and −10°C., and Mathlein (1938), in whose experiments the adults were generally the most resistant, and the eggs the least resistant stage at −2° and −6°C. The discrepancy may possibly be due to differences in the moisture content of the grain. Certainly, the moisture conditions during rearing and exposure are likely to be important, as with *C. granaria*, but they have not been specified except by Robinson (1926), who reared his beetles in grain of moisture content 13–14 per cent., and by Ushatinskaya (1950*a*), who used grain of moisture content 15–16 per cent. in her experiments. The figures in Table V show the exposure periods required to give complete mortality; a few (marked " S ") show the maximum survival periods observed.

TABLE V.

Exposure periods required to give complete mortality in *Calandra oryzae*.

Temp.(°C.)	Time to complete kill of :—				Author
	Adults	Pupae	Larvae	Eggs	
8·5	A month or so				Mathlein (1938)
6·5 to 7·5	A few weeks				,, ,,
5·5 to 6·5	A few weeks				,, ,,
About 7·2	17 days				Robinson (1926)
4·4 to 7·2	80 days				Back & Cotton (1924)
4·5 to 6	80 days (S)	35 days (S)		35 days (S)	Mathlein (1938)
5	21 days				Ushatinskaya (1950*a*)
1·7 to 4·4	18 days				Back & Cotton (1924)
0·5 to 5	Within a month				Mathlein (1943)
−1 to +1·7	16 days				Back & Cotton (1924)
0±	7·5 days	16 days	17 days	Over 7 days	Ushatinskaya (1950*a*)
0	16 days (S)				Mathlein (1938)
−1	8–16 days		11 days	4 days	Back & Cotton (1924)
−2	9 days (S)	6–8 days (S)		4 days (S)	Mathlein (1938)
−4 to −1	8 days				Back & Cotton (1924)
−6·7 to −4	6 days				,, ,, ,, ,,
−5	4 days	4·5 days	3 days	12 days	Ushatinskaya (1950*a*)
−6	3 days				Zacher (1944)
−6	3 days	3 days		2 days	Mathlein (1938)
−9·4 to −6·7	3 days				Back & Cotton (1924)
−10	15 hours	27 hours	24 hours	90 hours	Ushatinskaya (1950*a*)

Callosobruchus analis and *C. chinensis*.

These cowpea beetles are adapted to warm climates, and did not survive in our experiments. They were not tested in B7–10.

Carpophilus dimidiatus.

This beetle failed in a series of tests including B10. In the absence of evidence to the contrary, it seems probable that this really is a cold-susceptible species. Unlike the other two species of *Carpophilus* in our experiments (see below), it lives on fairly dry materials. It is the only one of the three not recorded out-of-doors in Britain away from storage places, and it is omitted by Joy (1932), although he includes the other two species in his Handbook.

Carpophilus hemipterus and *C. ligneus*.

We are inclined to discount the failure of these dried-fruit beetles in B2 and of *C. hemipterus* in B6. The moist cultures became mouldy before the end of the experiment, and the dry ones were probably too dry.

C. hemipterus was found in a rotten branch by Walker (1907) at Bagley Wood, near Oxford, and it is regarded as being established in Britain (Hinton, 1943*c*), though the latter point is not in itself proof of cold-hardiness. Allen (1941) found both species in the open at Windsor. While it seems more likely that these specimens are established in the open than that their presence was due to the flight of beetles from houses or from distant storage places, the latter possibilities cannot be dismissed. Strong (1936) reported observations showing that *C. hemipterus* can travel over 2 miles in 4 days.

Caryedon fuscus.

Although the Groundnut Beetle is an insect of warm regions, one individual survived in B6. No tests were made under milder conditions.

This species must develop only very slowly in unheated conditions in Britain. R. W. Howe, in a paper soon to be published, shows that it does not complete its development at constant temperatures below about 18°C., and takes about 70 days at 20°C.

transfer
p. 33

Caulophilus latinasus.

The Broad-nosed Grain Weevil failed in both of Mansbridge's experiments, and should probably be classed as cold-susceptible.

Dermestes frischii.

Our experiments show that larvae and adults of this widespread Hide Beetle can overwinter in Britain. It has been found in the field, on carrion (Duffy, 1945). In the severest of our tests, larvae survived but adults did not.

Dermestes lardarius.

This cosmopolitan species is well established in unheated buildings in Britain (*cf*. Freeman & Turtle, 1947; O'Farrell & Butler, 1948), and is a common inhabitant of pigeons' nests (Woodroffe, 1953). Kreyenberg (1928) noted that adults survived 24 hours at −3°C. Larvae and adults overwintered in the severest of our experimental conditions. Mansbridge (1936) stated that larvae do not survive, but this is contradicted by the result entered for one of his own two experiments. Hinton (1945, p. 282) wrote that: " Out of doors or in unheated buildings the winter is always passed in the adult stage (Kreyenberg, 1928; Canzanelli, 1935; Takio, 1937) . . .". The authors quoted wrote of Germany, Italy and Japan, respectively. From this it seems possible that the life-cycle may be so arranged that larvae do not occur in the winter, although our results show that they are well able to survive the cold.

Dermestes maculatus.

All stages of this cosmopolitan species are reported to overwinter in Japan (Kimura & Takakura, 1919) and in Germany (Kreyenberg, 1928). But it failed completely in Mansbridge's experiments and in all of ours except the mildest test (B10). This may be attributable to the effects of culture conditions or to permanent differences within the species, for it is found out-of-doors: Duffy (1945) collected larvae and adults from carrion, and adults have twice been recorded from Windsor Forest (Donisthorpe, 1939) and twice on carrion near Oxford (records held by Mr. Charles Elton, Bureau of Animal Population, Oxford). In earlier experiments at this Laboratory (T. A. Oxley, unpub.), probably with the same stock as we used, larvae died within 42 days at 18°C., 70 per cent. relative humidity.

Dorcatoma bibliophagum.

This book borer from South America failed to overwinter in 3 tests, one of them under relatively mild conditions.

Ephestia cautella.

Freeman (1948*a*) wrote that this moth could survive the winter "under specially favourable conditions in warmer parts of the country". O'Farrell & Butler (1948) thought the climatic conditions of N. Ireland prevented its establishment. Dr. J. A. Freeman and his colleagues of the Ministry of Agriculture, Fisheries and Food, Infestation Control Division, have a good deal of evidence that *E. cautella* can overwinter in some situations, and detailed work has been undertaken by them and at the Pest Infestation Laboratory to throw more light on this (*cf.* Dep. Sci. industr. Res., 1952, pp. 10, 11; also H. D. Burges, unpub.). So far as the present results go, they suggest that *E. cautella* does not easily overwinter, though it did so in the milder of Mansbridge's experiments.

Ephestia elutella.

The larvae of this pest, very widespread in temperate areas, overwinter in unheated buildings in England in a state of diapause (*e.g.*, Richards & Waloff, 1946; Freeman 1948*a*; Waloff, 1949). It is also known to overwinter in Germany (Mehl, 1940), where it is native according to Zacher (1939). It has been recorded from a hay-loft in Belgium by Leclercq (1946), who refers to it as a field species living on grasses and other meadow plants, and according to Ford (1949) it is sometimes abundant in old haystacks in Britain. But O'Farrell & Butler (1948) found that most infestations in N. Ireland failed to become permanently established. The fact that it died out in the most severe of our tests suggests that it would fail to survive in some situations in a severe winter; yet Waloff found that diapausing larvae all survived at −2°C., 55 per cent. relative humidity, for 40 days (all were killed after 51 days). It may be relevant that our insectary stock differs from some others in having no diapause phase when kept at 25°C. (Waloff, 1949), though in this respect it resembles another stock recently collected from a warehouse.

In experiments with eggs and larvae of *E. elutella*, Bovingdon (1933) found they were all killed in 7 days at −3° to −4°C., or at −6° to −7C., or in 18 hours at −10° to −11°C.

Ephestia kuehniella.

The larvae of the cosmopolitan Mill Moth are known to overwinter in unheated warehouses (Freeman & Turtle, 1947), though it does much better in heated premises such as mills and bakeries. O'Farrell & Butler (1948) write that it does not thrive in unheated premises and does not establish itself in unheated buildings in N. Ireland. In our experiments, the larvae survived the most rigorous conditions. Mathlein (1943) noted the survival of *E. kuehniella* after nearly 4 months in materials at 0·5° to 5°C. Kunike (1939) found that old larvae and the pupae could withstand temperatures down to 0°C. for several months; the young larvae were less resistant, and the eggs still less so. The following treatments have been cited as sufficient to kill all stages (except Zacher's figure, which refers to eggs only). Cotton does not state how his figures were arrived at.

116 days at −3·9° to −1·1°C. : Cotton (1950, p. 52)
14 days at −4° to −3°C. : Bovingdon (1933)
12 days at −4·7°C. (eggs only) : Zacher (1944)
24 days at −6·7° to −3·9°C. : Cotton (1950, p. 52)
11 days at −7° to −6°C. : Bovingdon (1933)
7 days at −9·4° to −6·7°C. : Cotton (1950, p. 52)
4 days at −12·2° to −9·4°C. : Cotton (1950, p. 52)
75 hours at −11° to −10°C. : Bovingdon (1933)
3 days at −15° to −12·2°C. : Cotton (1950, p. 52)
1 day at −17·8° to −15°C. : Cotton (1950, p. 52)

Galleria mellonella.

The larvae of the Wax Moth are cold-hardy, as shown by the survival of some in one of our severest tests, A0.

Gibbium psylloides.

This cosmopolitan Ptinid is long established in Britain (Hinton, 1941). The survival of larvae was demonstrated in A4 and other experiments, that of adults in one of the severest tests (A0).

Gnathocerus cornutus.

Of this cosmopolitan Flour Beetle Freeman & Turtle (1947) write that it cannot overwinter in unheated stores (*cf.* O'Farrell & Butler, 1948), "its lower limit of temperature being about 50°F." It failed in Mansbridge's experiments and in ours, including the very mild and brief B10. However, Joy (1932) describes it as common under bark, chiefly elm, and Mr. Charles Elton has a record of its emergence from a piece of dying elm brought in from an Oxford garden.

Gnathocerus maxillosus.

This beetle, sometimes introduced here from warm regions, is evidently very susceptible to cold: like *G. cornutus*, it failed even in B10.

Hofmannophila pseudospretella.

Mansbridge (1936) exposed larvae and found some at least survived. Since this is a common native species, such a result is to be expected.

Laemophloeus ferrugineus.

Since this cosmopolitan grain beetle is native to Britain, and common in unheated warehouses, the survivals in the three experiments were not surprising. Since a number of adults survived in A0, their failure in A3 seems anomalous.

Laemophloeus minutus.

The Flat Grain Beetle, in contrast to *L. ferrugineus* and *L. turcicus*, failed in a series of relatively mild tests, including B9. Like *L. pusilloides*, it is adapted to warm climates, and flourishes otherwise chiefly in heating grain. Williams (1954) exposed all stages of *L. minutus* in a refrigerator at a temperature fluctuating from 2°C. down to 0·5°C. (occasionally to −0·5°C.), and found that some of each stage could survive 2·5 days' exposure, and some adults and pupae at least 4 days. These experiments are not very closely comparable with ours, so that it is not clear whether or not the two sets of results are compatible. Williams concludes that " the species can probably survive a normal winter in warehouse conditions in this country but may be killed off by an abnormally cold season ". O'Farrell & Butler (1948), on the other hand, wrote that in N. Ireland *L. minutus* " died out during the winter except in heated buildings or heated grain ". Our results seem more in keeping with the latter statement.

Laemophloeus pusilloides.

This grain beetle seems to be similar in its properties to *L. minutus* (see above); here it failed in the same series of experiments.

Laemophloeus turcicus.

In Britain this species is almost confined to mills; yet the results show it is cold-hardy. Larvae and adults survived in A2 and milder tests, failing only in A1.

Lasioderma serricorne.

The Cigarette Beetle is well known to be susceptible to cold, and there is a series of papers dealing with the lethal effects of various low temperature treatments. The following treatments are reported to give a complete kill of all stages:—

40 days at 4·4°C.: Strong (1936)
33 days at 4·4°C.: Swingle (1938), Reed & Vinzant (1942)
16 days at 2·2°C.: ,, ,, ,, ,, ,,
(But Powell (1931) states that eggs survived 20 days at 2°C.)
8 days at −4°C.: Swingle (1938)
1 day at −4°C.: Reed & Vinzant (1942)
(But according to Skalov (1931), larvae survived 6 days at −6° to −3°C., and 50% survived 2 days at −8°C.)
3 days at −10° to −5°C.: Skalov (1931).

In our experiments there were survivals only in B9 and B10. Larvae survived in both tests, and also adults in B10. The above figures suggest that B5 and B7 should have been survived. It may be that differences in moisture conditions account for this discrepancy, or that the insects' resistance is reduced by fluctuating temperatures. They failed also in Bx.

Latheticus oryzae.

O'Farrell & Butler (1948) wrote: " This species requires a high temperature, and survived only in a few of the hottest places in flour mills, e.g. near driers, boilers, etc. Only a few specimens occurred occasionally in oatmeal and provender mills ". In our A3 and B3 it failed completely, but larvae survived the very mild and brief B10.

Lepisma saccharina.

Mallis (1945) writes of this Silverfish: " It is believed to be originally a warm-country insect. It has adapted itself to living in temperate climates by dwelling in warm and humid areas, especially in basements, around water pipes, etc.". O'Farrell & Butler (1948) found it widespread in mills, warehouses and bakeries, not in granaries, but they classified it with the "species well adapted to live in unheated buildings". It is common in birds' nests (Woodroffe, 1953), and survived in the most rigorous of our experimental conditions.

Mezium affine.

Although this Ptinid is found in N. Africa as well as Britain (Hinton, 1941), it is quite cold-hardy, and numbers of larvae survived in A1. Howe & Burges (1953*a*) have also observed the overwintering of a population under relatively mild conditions, with the temperature never below 0°C.

Necrobia rufipes.

Although the Copra Beetle is repeatedly brought to Britain on various imports, it is adapted to hot climates and does not easily survive the British winter. Freeman (1948*b*) lists it together with *Ephestia cautella* and *Calandra oryzae*, as "surviving under specially favourable conditions in warmer parts of the country". Simmons & Ellington (1925) found the fully grown larvae were best able to withstand low temperatures. In our experiments, larvae survived in B10 and in Bx (Table III). There were no survivals in A0.

Niptus hololeucus.

Hinton (1941) describes this Ptinid as nearly cosmopolitan, but absent from the tropics. In Britain it is a long-established pest in stores and houses, and is found in nests of bees, wasps and birds (Howe & Burges, 1952*a*; Woodroffe, 1953). The experiments show that many larvae, and probably also adults, survived in A1 and A2.

Oryzaephilus mercator.

This grain beetle comes from hot regions, and was unable to survive in any of the experiments, even B10. This is one of the points of difference between *O. mercator* and the closely related *O. surinamensis*, which we have found to be cold-hardy (*cf.* Howe, 1953).

Oryzaephilus surinamensis.

Unlike *Oryzaephilus mercator*, this species is common in temperate as well as in warmer areas, and is well known to overwinter in unheated buildings in Britain (*cf.* Freeman & Turtle, 1947; O'Farrell & Butler, 1948); it is recorded from fungi (Joy, 1932). It survived even the most severe tests, except in Mansbridge's experiment (B1), where its failure seems unlikely to be attributable to cold; a possible cause was the presence of mites, mentioned by Mansbridge. Thomas & Shephard (1940) reported 50 per cent. survival after 30 days at 10°, or 105 hours at 2°C. In experiments by Back & Cotton (1926*b*), a small percentage of adults and larvae survived 3 weeks at $-1{\cdot}1°$ to $+1{\cdot}7°$C., but all stages were killed by exposure to $-6{\cdot}7°$ to $-3{\cdot}9°$C. for a week. Further figures are given by Cotton (1950, p. 52), without explanation of their origin.

← insert p
from p.

Palorus ratzeburgi.

This and also *P. subdepressus* (see below) are listed by O'Farrell & Butler (1948) among those "established in heated buildings, but able to survive the winter in small numbers in unheated buildings". Cold-hardy insects like *Tenebrio* and *Tenebroides* appear in this list, but of *Palorus* they write: "These species were able to maintain themselves in the cooler parts of the mills, where they lived mainly in deep accumulations of grain spillage infested by *Calandra* spp.". Butler (1949) writes: "The development of *P. ratzeburgi* is adapted to a relatively high temperature, and it probably resembles *T. castaneum* in this respect".

Yet, in his account of the beetles of Germany, Reitter (1911, p. 343), notes that *P. ratzeburgi* is found there under bark and in tree-litter, as well as in stored products. In view of this, its failure in three of our tests, including B6, seems unlikely to have been due only to cold. Besides the results shown in Table IV, one of 11 adults survived in Bx (Table III).

Palorus subdepressus.

We do not know of any record of this species having been found out-of-doors in Britain, and the above remarks of O'Farrell & Butler are only doubtful evidence of cold-hardiness. On the other hand, we discount the significance of its failure in our tests, because it was cultured on damp material which became mouldy before the end of the experiments.

Plodia interpunctella.

O'Farrell & Butler (1948) reported the failure of this cosmopolitan pest to establish itself in N. Ireland and considered this was probably due to the climatic conditions. However, Mansbridge (1936) found that larvae survived in his overwintering experiments, and in ours some survived even in A0. Dr. J. A. Freeman (*in litt.*) tells us that *Plodia* is established in silos in Avonmouth, Glos., and that it survived the relatively hard winter of 1941–42, among others, at the tops of grain silos at Preston, Lancs. Cotton (1950, p. 52) lists the following exposures to cold as being lethal to all stages: 90 days at −3·9° to −1·1°C., 28 days at −6·7° to −3·9°C., 8 days at −9·4° to −6·7°C., 5 days at −12·2° to −9·4°C., etc., but does not state their basis.

Pseudeurostus hilleri.

This Japanese Ptinid was first found in Britain in 1939 (Howe, 1940), and seems to be well established though not common (Hinton, 1941; O'Farrell & Butler, 1948). It overwintered readily in the most rigorous of our experimental conditions.

Ptinus fur.

This is a cosmopolitan species long established in Britain (*cf.* Hinton, 1941), where it is found not only in stores, houses, etc., but also in various birds' nests (Woodroffe, 1953). It survived in A1, and its failure in B2 must almost certainly have been due to factors other than cold. Howe & Burges (1951) remarked that *P. fur* probably overwinters in larval and resting adult stages, since larvae and adults can be found in stores at all seasons; there is a tendency for mature larvae in cocoons to go into diapause at low temperatures.

Ptinus sexpunctatus.

This species is native to Britain, and is often found in the nests of certain bees (Hinton, 1941), and of sparrows and martins (Woodroffe, 1953). It has been found in stored middlings and flour (Howe, 1949, 1950). Howe & Burges (1951) conducted an overwintering experiment and concluded that the species could survive the winter as young and mature larvae and as resting adults in cocoons. In our experiments, adults and larvae overwintered in B2; only a few came through in A1, but we suspect other factors than cold were causing damage.

Ptinus tectus.

This species is considered to have come from Tasmania, but it is now a widespread pest in temperate areas. In Britain it is very common in unheated warehouses, where it readily overwinters. It is also common in certain birds' nests (Woodroffe, 1953). Laboratory work has shown *P. tectus* to be very resistant to cold; *e.g.*, some survive up to 7 weeks at a temperature about −4·5°C. (Howe & Burges, 1953*b*, fig. 11). In our experiments there was a high survival rate even in A1.

Rhizopertha dominica.

The Lesser Grain Borer is an insect of warm regions. Freeman & Turtle (1947) write: " All stages are normally killed in the course of an English winter, unless the grain is heating or is stored under such conditions that its temperature remains high." O'Farrell & Butler (1948) class it among the insects which maintain themselves with difficulty even in heated buildings, in N. Ireland. It failed to survive in our experiments except the mildest (B9 and B10). In laboratory experiments, Dendy & Elkington (1920) found some adults survived 7 days at 0·6°C., but not 11 days at 0·6° to 2·2°C.

Nevertheless, some *R. dominica* survived the mild winters of 1948–49 and 1949–50 in stacks of bagged barley stored in Romney Huts (constructed of a single layer of corrugated iron) at an airfield in Lincolnshire (Dr. J. A. Freeman, *in litt.*). No heating was detected.

Sitotroga cerealella.

Freeman (1948*a*) listed this grain moth among the frequently introduced species unable to overwinter in unheated conditions, and a similar impression is gained from the remarks of O'Farrell & Butler (1948) with respect to N. Ireland. But in our experiments at least a few survived fairly rigorous winter conditions (A3, A4).

Stegobium paniceum.

This cosmopolitan beetle is a common pest in retail shops, larders, etc., in Britain (*cf.* Freeman & Turtle, 1947), and has been found abundantly in pigeons' nests (Woodroffe, 1953). The fact that some survived in A0 contrasts with its failure in Mansbridge's B1, and shows that this is a cold-hardy insect. Warehouse observations support the view that it is very cold-hardy (Dr. J. A. Freeman, *in litt.*). Mathlein (1943) noted the survival of *Stegobium* after nearly 4 months in materials stored at 0·5 to 5°C.

Stethomezium squamosum.

This Ptinid appears to be an African species and it has not been found in warehouses in Britain (Hinton, 1943*a*; Howe & Burges, 1952*a*). In our experiments it failed to survive the severest conditions, but some adults, at least, survived less rigorous conditions (B2), so that the species might often overwinter in this country if introduced.

Tenebrio molitor.

This is one of the species O'Farrell & Butler (1948) refer to as " able to survive the winter in small numbers " in N. Ireland; but there seems to be no evidence that the larvae have any difficulty in overwintering. Large numbers were found inhabiting the recesses of a granary (Coombs, 1955), and it is commonly found in birds' nests (Woodroffe, 1953). In our experiments it survived even in A1. Some idea of the limits of its cold-hardiness may be gained from the figures given below (see also Mathlein, 1943).

Tenebrio obscurus.

In reference to N. Ireland, O'Farrell & Butler (1948) listed *T. obscurus* among the species which did not survive in unheated buildings. However, Mansbridge's experiments and also ours, especially A0, show that this species is well able to overwinter. This is in keeping with other evidence that *T. obscurus* is not much less cold-hardy than is *T. molitor*. Cotton & St. George (1929) showed that while *T. molitor* is confined to the northerly half of the U.S., and *T. obscurus* occurs in the southern parts, the latter is also found in the north along with *T. molitor*. They reported that larvae of both species were killed by 24 hours at 0°F. (–18°C.), but still showed signs of life after more than 7 months at 30° to 35°F. (–1·1° to +1·7°C.). But while *T. molitor* larvae were still not quite dead after 3 weeks at –15° to –12·2°C., 4 days under these conditions killed *T. obscurus*. Adults, pupae and eggs were less resistant. In *Tenebrio* it is the larval stage which overwinters, whereas in many other Tenebrionids living in temperate climates the winter is passed in the adult stage (Butler, 1949).

Tenebroides mauritanicus.

This cosmopolitan pest is known to overwinter in unheated warehouses in Britain (Freeman & Turtle, 1947). According to Cotton (1923), adults of the Cadelle and larvae in all stages pass the winter in the U.S.A. in hibernation, but apparently it does not overwinter in the pupal stage. Back & Cotton (1926*a*) wrote that the eggs and pupae are readily killed by cold, but that the larvae and adults are very resistant, and survived several weeks at –9·4° to –6·7°C. Our experiment confirms the cold-resistance of the larvae and adults. O'Farrell & Butler (1948) list this species among those " established in heated buildings, but able to survive the winter in small numbers in unheated buildings ". The description is somewhat misleading, since these authors seem not to distinguish between small numbers due to difficulty in overwintering and small numbers due to other causes.

Tinea spp. (casebearers).

Since these species live out-of-doors in Britain, it is not surprising that there was a high survival rate even under the most rigorous of our experimental conditions.

Tinea granella.

Corbet & Tams (1943) give the distribution of this moth as Europe and Japan. Zacher (1939) lists it as native to Germany. It is listed by O'Farrell & Butler (1948) among the resident species of restricted or infrequent occurrence in the stores of N. Ireland. In our single experiment, under fairly severe conditions (A3), a small percentage survived the winter.

Tineola bisselliella.

The Clothes Moth is a resident species, and is found in sparrows' nests (Woodroffe & Southgate, 1951). In our experiments, numbers of larvae survived even in A1. Back & Cotton (1926*c*) reported the survival of larvae after 67 days at –6·7° to –3·9°C., or 21 days at –15·0° to –12·2°C.

Tribolium castaneum.

Good (1936) writes: " *T. castaneum* is essentially an insect of warm climates, and, although sometimes recorded from Canada and other northern countries, it is evidently not a permanent resident north of the fortieth parallel in eastern United States except in heated buildings ". It is said to be less resistant to cold than *T. confusum* (Freeman & Turtle, 1947). O'Farrell & Butler (1948) list *T. castaneum* among the species which maintain themselves with difficulty even in heated buildings, in N. Ireland. Nevertheless, it can overwinter at times in large stacks of material (*cf.* p. 322).

In the present experiments it failed even in B9, in which some *T. confusum* survived, although some larvae survived in the still milder B10.

In laboratory experiments, H. D. Burges has found that while some larvae survived up to 20 weeks at 10°C., all stages were killed within a week at 0°C. (Dep. sci. industr. Res., 1951). It has been noted that all stages have died out in a month in material stored at 0·5 to 5°C., or 2 to 3°C. (Mathlein, 1943, 1948). Cotton (1950, p. 52) gives the same lethal exposures as he cites for *T. confusum* (see below), except for 8 days instead of 12 at –3·9° to 1·1°C.

Tribolium confusum.

This is sometimes regarded as a temperate species, and in the United States it is commoner in the north than *T. castaneum*, which predominates in the south (Good, 1936). But it does not normally overwinter in unheated buildings in Britain (Freeman & Turtle, 1947; O'Farrell & Butler, 1948). Our experiments tend to confirm this, since the only survivors were in the very brief B9. Freeman & Turtle (*loc. cit.*) write that all stages die after exposure at 7·2°C. for 25 days. Nagel & Shepard (1934) found 22 days at 7°C. or 1 day at –6°C. killed all stages. The following are the exposures listed by Cotton (1950, p. 52) as required to kill all stages: 17 days at –1·1°C., 12 days at –3·9° to –1·1°C., 5 days at –6·7° to –3·9°C., 1 day at –9·4° to –6·7°C. or lower. He does not state how these figures, and the similar ones for *T. castaneum*, were arrived at.

Tribolium destructor.

Hinton (1948) gives the distribution of this flour beetle as Africa, Europe, and N. America. It died in A3, B3 and Bx, but adults survived in the very mild and brief B10. Mathlein (1943) found that an infestation died out within a month at 0·5 to 5°C.; all developmental stages died within 40 days at 3·5°C., or 10 days at –2°C.; adults and larvae died within 3 days at –6°C.

Trichophaga tapetzella.

This is a resident species. In experiments A3 and A4, it was noticed that a number of larvae remained active throughout the winter. There were a number of survivors even in A0.

Trigonogenius globulus.

This cosmopolitan species was first recorded in Britain over 50 years ago, and is now fairly common, though not abundant, in storage places and in pigeons' nests (Howe & Burges, 1952*a*). In our experiments, some survived even in A1.

Trogoderma granarium.

Hinton (1945) describes this Dermestid as coming originally from India, Ceylon and Malaya. Nevertheless, both adults and larvae are very resistant to cold, as shown by their survival in the most rigorous of our tests. In addition, our colleague Mr. H. D. Burges found less than 4 per cent. mortality in larvae exposed in a screen from 21st July 1953 to 5th May 1954, a period which included a severe cold spell with minima below –3°C. on 11 consecutive days, and below –8°C. on 3 days. Voelkel (1924) tested its resistance to cold and found that although the larvae became motionless at 8°C., they could tolerate 2° to 4°C. for 12 months without damage, while most could survive 72 hours at –10°C.: intermittent cooling killed more than did an unbroken exposure. It has been observed to overwinter in unheated stores (Dr. J. A. Freeman, *in litt.*).

Somewhat as in the case of *Anthrenus vorax*, this species seems to be almost confined to heated premises (particularly maltings) in Britain because the *summer* temperatures are high enough only for an extremely protracted life-cycle. Mr. H. D. Burges has observed its slow rate of development in outdoor conditions over the summer. From 4th April 1953 to 21st October 1954, 30 moderate to large-sized larvae produced only 2 adults, which died in the larval skins, and 5 pupae, of which 3 were dead. At a constant temperature of 20°C., 45 large larvae remained in that stage for over 145 days, before the first pupa was formed. Hadaway (in press) found the larval period took more than 12 months at 20°C. (Voelkel, 1924, recorded a larval period of only 47 days at 20°C.).

Trogoderma versicolor.

Hinton (1945) describes this species as " nearly cosmopolitan ". The high resistance of the larvae to cold is shown by their survival in A1. Hadaway (in press) found that development was so slow at 20°C. that most did not reach the pupal stage in 8 months.

General Discussion.

Besides the foregoing comments on the results for each species, some more general points emerge when the results are viewed as a whole.

In earlier sections we compared the temperatures in different situations and in different winters, after summarising them in various ways. Taking account of these and of the biological results, we may group the species as in the lists on p. 345. As in Table IV, a species is recorded as surviving in a given set of conditions even if it is just able to tolerate them, so that there are a few survivors in a culture.

1. It may be noted, first of all, that the results are generally consistent with the arrangement of the series of exposures in the order indicated by the symbols. That is to say, the order of severity as determined by an examination of the temperature figures corresponds with the order of severity as assessed from the effects on the survival of the insects. There were a few exceptions, as indicated by the notes in parentheses in the lists. This is not surprising in view of the small degree of difference between some of the exposures, and the fact that they come in slightly different order when the temperatures are dealt with in different ways (*cf.* Tables II and III).

2. Even so, some, perhaps all, of the exceptions were more likely due to failures in certain cultures from causes other than cold alone. A failure to overwinter is a less reliable result than success, and needs to be checked by repeated experiments: it is notoriously difficult to establish a negative. For example, a misleading negative result may arise from the use of an unusually susceptible strain of the species, or of inadequate numbers; the cultures may become too dry, or become infested by moulds as in the cases referred to below; or mites may get in, as they did in some of Mansbridge's experiments (and perhaps gave rise to some of the anomalous failures in his B1). Any survivals, on the other hand, can be accepted without reservations, since they show it is possible for at least one strain of the species concerned to withstand the conditions of the test. The proportion surviving is significant as an indication of whether the species survives readily or with difficulty, but it may be reduced by other factors than cold.

3. Nine of the species are shown in parentheses because there is reason to believe that they are probably hardier than our results indicate. Five of these, as noted in the Detailed Comments (above), have been recorded from out-of-doors situations in Britain, in circumstances strongly suggesting that they must be able

I. Very Susceptible

Fail B10.

(Alphitobius laevigatus)
Carpophilus dimidiatus
(Gnathocerus cornutus)
Gnathocerus maxillosus
Oryzaephilus mercator

II. Moderately Susceptible

(a) Survive B10, fail B9.

Calandra oryzae
(Dermestes maculatus)
Tribolium castaneum

(b) Survive B9, fail B8.

Araecerus fasciculatus
Tribolium confusum

(c) Survive B8, fail B7, 6, 5 or x.

(Calandra granaria)
Ephestia cautella

(d) Survive B7, 6, 5 or x, fail B2 or B1.

Caryedon fuscus
(Palorus ratzeburgi)

III. Moderately Hardy

Survive B2, B1, A4, or A3, fail A2, A1 or A0.

Blatta orientalis
Sitotroga cerealella
Stethomezium squamosum

IV. Hardy

Survive A2, A1 or A0.

Anthrenocerus australis
Anthrenus verbasci
Anthrenus vorax (failed A2, B6)
Attagenus megatoma
Attagenus pellio
Dermestes frischii
Dermestes lardarius
Ephestia elutella (failed A1)
Ephestia kuehniella
Galleria mellonella
Gibbium psylloides
Laemophloeus ferrugineus
Laemophloeus turcicus (failed A1)
Lepisma saccharina
Mezium affine
Oryzaephilus surinamensis (failed B1)
Plodia interpunctella
Niptus hololeucus
Pseudeurostus hilleri
Ptinus fur
Ptinus sexpunctatus
Ptinus tectus
Stegobium paniceum (failed B1)
Tenebrio molitor
Tenebrio obscurus
Tinea columbariella
Tinea pellionella
Tineola bisselliella
Trichophaga tapetzella
Trigonogenius globulus
Trogoderma granarium
Trogoderma versicolor

Species whose Position in the above List was incompletely determined

I or IIa.

Laemophloeus minutus
Laemophloeus pusilloides

I, IIa or IIb.

Caulophilus latinasus

I, IIa, IIb or IIc.

Acanthoscelides obtectus
Ahasverus advena
Callosobruchus chinensis
(Carpophilus hemipterus)

I or II.

(Alphitobius diaperinus)
Callosobruchus analis
(Carpophilus ligneus)
Dorcatoma bibliophagum
(Palorus subdepressus)
Periplaneta americana

IIa, IIb, or IIc.

Latheticus oryzae
Tribolium destructor

IIb or IIc.

Lasioderma serricorne
Rhizopertha dominica

IId or III.

Necrobia rufipes

III or IV.

Achroia grisella
Hofmannophila pseudospretella
Tenebroides mauritanicus
Tinea granella

to overwinter. These species are *Alphitobius diaperinus*, *A. laevigatus*, *Carpophilus hemipterus*, *C. ligneus* and *Dermestes maculatus*. The first four need to be kept under very moist conditions, and the food material became mouldy before the experiments were finished; they were also kept on an alternative medium (*cf.* Table IV), but this was probably too dry for them. A fifth species, namely *Palorus subdepressus*, was kept only on moist material which became mouldy in due course; the significance of its failure must therefore remain in some doubt, although we have no evidence that it is cold-hardy. Another species, *Palorus ratzeburgi*, gave results indicating a moderate susceptibility to cold, yet it is recorded as living out-of-doors in Germany. It was not cultured on moist material, and the cultures were free of mould except for a slight growth in one of the four tests.

It may be that some of the insectary stocks had become unduly susceptible to cold. This seems to have happened in the case of *Calandra granaria*, which is shown in a position signifying much less resistance to cold than is indicated by the work of most other authors (*cf.* p. 334 and fig. 4). The same may apply to *C. oryzae*, for observation suggests that it overwinters a little more readily than our results show (Dr. J. A. Freeman, *in litt.*). Of course, it is possible that such cold-susceptible strains also occur in granaries and stores and even in more natural situations.

4. In the list on p. 345, nearly half the species fall into one group (Group IV: Hardy), while the others form a series of small groups of successive degrees of hardiness or susceptibility. The large size of the "hardy" group may be an indication that the conditions were not cold enough to bring out most of the differences between species in this group. Perhaps if our experimental period had included a winter as cold as that of 1946–47, further sub-division of the group would have been possible. As it is, we have only three failures in A1, or A2, and some observations on the numbers of survivors of the different species, to suggest some of the differences which may exist.

5. The records of survivals reflect the overwintering ability of the hardiest stage tested, and are not necessarily a good guide to the hardiness of the other stages. In the majority of species the larva seemed to be the most cold-resistant stage, though this might not so often have been the case if shorter and more intense exposures had been used. In a number of beetles, adults as well as larvae succeeded in overwintering. In a few cases, notably *Calandra*, the adult is known to be the most resistant stage, but our experiments did not illustrate this point; in *C. granaria*, for example, it was shown that adults did overwinter in some tests (Table IV, col. 6, left-hand section) but it was not shown that other stages failed to do so in these tests, hence there is no entry in the right-hand section of col. 6. One interesting result was the survival of larvae of *Dermestes lardarius* in our experiments, in spite of statements in the literature that larvae do not overwinter (*cf.* p. 335).

6. To a considerable extent the ability or failure of species to overwinter can be related to the place of origin and the world distribution of the species concerned, so far as these are known. Many examples are noted in the Detailed Comments on the results. Thus in the "very susceptible" and "moderately susceptible" groups are found species such as *C. oryzae* *, *Laemophloeus pusilloides* and *Tribolium castaneum*, coming from hot climates. The "hardy" group includes species which are native to an area including Britain, or have at least been established out-of-doors in this country for a long time, *e.g.*, *Anthrenus verbasci*, *Attagenus pellio*, *D. lardarius*, *Ptinus fur*, *P. sexpunctatus*, *P. tectus*

---

* Possibly *C. oryzae* is generally a little hardier than our results indicate (*cf.* p. 334).

(first recorded in 1892), *Tenebrio molitor*, *Tinea pellionella*, and *Tineola bisselliella*.

Since these relationships are to be expected, it is perhaps more interesting that a certain number of contrary cases have also been found. Several species coming from warm climates and obviously well adapted to live in them, nevertheless show also a considerable degree of cold-hardiness. These include *Trogoderma granarium* and *Anthrenus vorax*, and some less clear examples such as *Mezium affine*, *Tenebrio obscurus*, *Anthrenocerus australis*, *Blatta orientalis*, and *Plodia interpunctella*.

7. The classification outlined on p. 345 corresponds fairly well with the conception of overwinterers, non-overwinterers and intermediates referred to in the Introduction (p. 312). Insects in the " hardy " group are known, or may be confidently expected, always or nearly always to survive the winter in unheated buildings in Britain. Those in the " very susceptible " group and most of those in the " moderately susceptible " group would normally survive the winter only in heated buildings or in materials heating through the activity of insects or micro-organisms. or retaining their summer temperature in the depths of a bulk. Those in the " moderately hardy " group would sometimes survive the winter in unheated conditions, and sometimes fail, according to the severity of the winter, the degree of protection afforded by the building, foodstuff, etc. Obviously these categories based on the complex situations and chains of events in storage places cannot be sharply defined, and therefore no complete correspondence between the two classifications can be expected. Nevertheless the comparison is important, and it is the aim of the present work to contribute towards making it as definite and as detailed as possible. When more is known about the overwintering powers of all the species concerned and about the temperature conditions in warehouses, a much fuller correspondence between these two sets of information will no doubt be established. In the meantime, the sketchy picture presented here will be useful.

Our results show that *Laemophloeus ferrugineus*, *Sitotroga cerealella* and *T. obscurus* do not belong among the non-overwinterers where Freeman (1948*a*) placed them. On the other hand, Freeman's classification of *C. granaria* and (less clearly) *C. oryzae* must be given more weight than our negative results. Similarly, our results with the two species of *Palorus* cannot be taken as proof that O'Farrell & Butler (1948) were wrong in placing them (although with qualifications which may be important) among the overwintering species.

8. Of course, resistance or susceptibility to cold is not the only factor determining the presence or absence of a pest in a given region or its status as a pest. In heated buildings, or in the period between their importation and the onset of winter, many of the " susceptible " species flourish in Britain and at times do considerable damage. Some of them are well established even in colder areas. Finally, some species which cannot stand a complete winter may survive if imported in February or March.

On the other hand, species capable of overwintering in unheated buildings may find other features of the climate unsatisfactory. As we have noted above, the high temperature requirements of *A. vorax*, particularly the pupa, may not easily be fulfilled in a British summer. The larvae of this species and of *T. granarium* and *T. versicolor* would all develop extremely slowly in unheated buildings in Britain, and *Oryzaephilus surinamensis* is also rather poorly equipped in this respect. Many of the species in the " susceptible " groups must likewise be seriously handicapped by the overall coolness of our summer; this certainly applies to *Tribolium castaneum*, *Rhizopertha dominica*, *Oryzaephilus mercator* and *Lasioderma serricorne*.

In the Detailed Comments, we noted that a number of species had greater difficulty in establishing themselves in N. Ireland (according to O'Farrell & Butler, 1948) than in England (according to Freeman & Turtle, 1947, and others). Whatever the reason for this may be, it can scarcely be in the relative severities of the winter in the two places. For example, Bilham (1938, p. 156) shows that the mean January temperature is about 41–42°F. for N. Ireland, which is warmer than the greater part of England. On the other hand, the mean July temperature is about 58–60°F., which is cooler than that for any part of England except the extreme north (*cf.* Bilham, p. 157; all the figures quoted above are reduced to sea-level values). It seems possible that the cooler summers, on average several degrees F. cooler than those of south-eastern England, may be a significant influence on the prevalence of certain pests.

Pests naturally tend to be more abundant in warm conditions than in cold, owing to the higher rate of increase and the fact that the time available in either for uninterrupted increase is usually limited by measures of hygiene or control. Hence it does not follow that a species which is more abundant in heated premises has difficulty in withstanding the cold. This point was made above in reference to some of the pests discussed by O'Farrell & Butler (1948). A related point is that many species prefer warm to cold conditions and seek out the former if they can. This may be a factor affecting the distribution of such species as *Ephestia kuehniella*, *Laemophloeus turcicus*, *Stegobium paniceum*, *T. granarium*, *Anthrenus vorax*, *Anthrenocerus australis* and *Lepisma saccharina*, which fall in the "hardy" group, yet are much more characteristic of warmed premises.

9. There is no precise information about the cold-resistance of most of the storage pests. and much more laboratory work is needed to produce it. Another little-known aspect of the subject is the physiology of cold-resistance. Generally, we do not know to what extent storage pests become hardier as a result of exposure to cold, nor do we know anything of the relative effect of sudden as against gradual falls in temperature; the few species for which something is known are mentioned on p. 314. Other unknown factors are the effects of fluctuating as compared with constant temperatures, the effects of differences in the conditions before the exposure to cold, the extent to which successive cold periods may have a cumulative effect, and the speed and completeness of recovery from sub-lethal exposures.

The present work can contribute little towards the study of these questions; they call for more closely controlled experiments, on one species at a time. Such experiments can provide the basis for the interpretation of results like these we have presented; for while these results provide means of explaining (and sometimes predicting) a set of ecological observations, on the physiological level they are themselves observations requiring analysis.

Summary.

In order to test their ability to survive the winter in unheated buildings, 68 species of storage and domestic insect pests were exposed throughout one or more winters in wooden screens and various outbuildings at the Pest Infestation Laboratory, Slough, Bucks.

Generally. cultures containing all developmental stages were exposed. The chief aim was to demonstrate some survival or else the complete failure of the culture; conclusions about single stages were added where possible.

The ability or failure of a species to overwinter may be affected by the following factors, which are discussed: cold-hardiness, effects of previous conditions, differences between strains or races within a species, severity of the winter, length of period of exposure, moisture conditions, type of building, protection by materials in storage, biological heating of the immediate environment.

The shortest experiment lasted 16 days, the majority for about six months.

The lowest temperatures varied from +3°C. to −10°C. Thermohygrographs were maintained alongside the experimental cultures. For an assessment of the relative severity of the winters concerned, the mean daily minimum temperature over the three coldest months was calculated from the meteorological records. A similar figure was worked out for the run of temperatures in each experiment, to give an index of the influence of the buildings, cupboards, etc., in the experimental exposures. Further comparative data are provided by records of the number of days when the temperature fell to or below certain levels, and of the longest periods at or below these levels, and by graphs. The order of severity of the different exposures as determined in this way is generally compatible with the biological results.

Nearly half the species survived even the severest tests and are classified as "hardy". Three were shown to be slightly less resistant and are classified as "moderately hardy". Thirteen "moderately susceptible" species are divided into four groups differing in hardiness. Five "very susceptible" species failed even in the mildest test. All the species are arranged as precisely as possible on this basis.

There are some anomalous results, due either to the use of unusually susceptible strains of insects or to failure from other causes. Because of this tendency, survivals are more significant and reliable than negative results. A few failures are discounted because the species concerned have been recorded from woods, etc., and therefore probably overwinter. The stock of *Calandra granaria* (L.) used in the experiments was less resistant to cold than is usual for this species. Two other results not in accordance with published statements were the failure of *Dermestes maculatus Deg.* (except in the mildest test) and the survival of larvae of *D. lardarius L.*

The "hardy" group includes species long established out-of-doors in Britain; the "susceptible" groups include species coming from hot regions. But some species adapted to life in warm regions are nevertheless cold-hardy, notably *Anthrenus vorax* Waterh. and *Trogoderma granarium* Everts. Some species characteristically found in heated premises are cold-hardy, *e.g.*, the above two and *Ephestia kuehniella* Zell., *Anthrenocerus australis* (Hope), *Lepisma saccharina* L., *Laemophloeus turcicus* Grouv., and *Stegobium paniceum* (L.). Their absence or scarcity in unheated buildings is attributable not only, if at all, to lethal effects of cold, but presumably to other factors such as a preference for warm places and a more rapid increase there.

The "hardy" insects would always or nearly always be able to survive the winter in unheated buildings. Most of the "susceptible" insects would normally survive the winter only in heated buildings or in materials heating through the activity of insects or micro-organisms or retaining their summer temperature in the depths of a bulk. The intermediate residue of species would sometimes survive the winter in unheated conditions, and sometimes fail, according to the severity of the winter and the degree of protection given by the building and by the infested material.

More information is needed about the temperatures prevailing under storage conditions. On the biological side, work is needed to determine in more detail the cold-resistance of individual species, and to investigate the effects of exposure on resistance, the effects of sudden as against gradual falls in temperature, the effects of fluctuating as against constant temperatures, the effects of previous conditions (food, moisture, etc.), the powers of recovery from successive short exposures to cold, and related matters.

Acknowledgements.

The senior author has been responsible for the planning and writing up of the work, the junior author for carrying out the practical work, and both for the interpretation of the detailed results. We are indebted to a number of our colleagues who have helped in various ways. Miss M. B. Hyde, Mr. A. M. Cunnington and Mr. H. D. Burges provided some of the thermohygrograph records, Miss S. M. Nightingale helped with the practical work, Mr. J. H. Hammond and Miss A. M. Stott provided the photographs. Messrs. R. W. Howe, G. E. Woodroffe, C. W. Coombs and H. D. Burges suggested additions or improvements to the manuscript.

We are particularly indebted to Dr. J. A. Freeman, who contributed a number of useful comments from the experience of the Infestation Control Division of the Ministry of Agriculture, Fisheries and Food.

We wish to thank Mr. Charles Elton, F.R.S., Director of the Bureau of Animal Population, for a number of unpublished field records from the Oxford Ecological Survey, several of them referred to in these pages.

The work forms a part of the programme of the Pest Infestation Laboratory and is published by permission of the Department of Scientific and Industrial Research.

References.

ALLEE, W. C., EMERSON, A. E., PARK, O., PARK, T. & SCHMIDT, K. P. (1949). Principles of animal ecology.—837 pp. Philadelphia, Saunders.

ALLEN, A. A. (1941). *Carpophilus hemipterus* L. and *C. ligneus* Murray (Col., Nitidulidae) at Windsor in the open.—Ent. mon. Mag., **77,** p. 201.

ALLEN, A. A. (1948). A note on the habitat of *Alphitophagus bifasciatus* Say, etc. (Col., Tenebrionidae).—Ent. mon. Mag., **84,** p. 46.

ANDERSEN, K. T. (1938). Der Kornkäfer (*Calandra granaria* L.), Biologie und Bekämpfung.—Monogr. angew. Ent., no. 13, 108 pp.

ASAHINA, E., AOKI, K. & SHINOZAKI, J. (1954). The freezing process of frost-hardy caterpillars.—Bull. ent. Res., **45,** pp. 329–339.

BACK, E. A. & COTTON, R. T. (1924). Relative resistance of the Rice Weevil, *Sitophilus oryzae* L., and the Granary Weevil, *S. granarius* L., to high and low temperatures.—J. agric. Res., **28,** pp. 1043–1044.

BACK, E. A. & COTTON, R. T. (1926*a*). The Cadelle.—Dep. Bull. U.S. Dep. Agric., no. 1428, 41 pp.

BACK, E. A. & COTTON, R. T. (1926*b*). Biology of the Saw-toothed Grain Beetle, *Oryzaephilus surinamensis* Linné.—J. agric. Res., **33,** pp. 435–452.

BACK, E. A. & COTTON, R. T. (1926*c*). Insect control in upholstered furniture.—Furn. Warehouseman, **6,** no. 5, repr. 7 pp.

BILHAM, E. G. (1938). The climate of the British Isles.—London, Macmillan.

BOVINGDON, H. H. S. (1933). Report on the infestation of cured tobacco in London by the Cacao Moth *Ephestia elutella* Hb.—Rep. Emp. Mktg Bd, no. 67, 88 pp.

BUTLER, P. M. (1949). Observations on the biology of *Palorus ratzeburgi* Wissman, with comparative notes on Tenebrionidae in general (Coleoptera).—Trans. R. ent. Soc. Lond., **100,** pp. 249–273.

CANZANELLI, A. (1935). Il *Dermestes lardarius* L.—Boll. Sez. ent. R. Oss. fitop. Milano, **6,** pp. 19–65. (From Hinton, 1945.)

COLHOUN, E. H. (1954). Temperature acclimatization in insects.—Nature, **173,** p. 582.

COOMBS, C. W. & FREEMAN, J. A. (1955). Insect fauna in an empty granary.—Bull. ent. Res., **46**, pp. 399–417.

CORBET, A. S. & TAMS, W. H. T. (1943). Keys for the identification of the Lepidoptera infesting stored food products.—Proc. zool. Soc., (B) **113**, pp. 55–148.

COTTON, R. T. (1923). Notes on the biology of the Cadelle, *Tenebroides mauritanicus* Linné.—J. agric. Res., **26**, pp. 61–68.

COTTON, R. T. (1949). Control of insects under corn storage conditions.—*In* What's news in the production, storage and utilization of hybrid seed corn, pp. 17–56. (Issued by Amer. Seed Trade Ass., Hybrid Corn Div.)

COTTON, R. T. (1950). Insect pests of stored grain and grain products.—Revd. edn., 244 pp. Minneapolis, Minn., Burgess.

COTTON, R. T. & ST. GEORGE, R. A. (1929). The Meal Worms.—Tech. Bull. U.S. Dep. Agric., no. 95, 37 pp.

DENDY, A. & ELKINGTON, H. D. (1920). Report on the vitality and rate of multiplication of certain grain insects under various conditions of temperature and moisture.—Rep. Grain Pests Comm. roy. Soc., no. 7, 52 pp.

DEPARTMENT OF SCIENTIFIC & INDUSTRIAL RESEARCH (1951). Pest infestation research 1949.—34 pp. London, H.M.S.O.

DEPARTMENT OF SCIENTIFIC & INDUSTRIAL RESEARCH (1952). Pest infestation research 1950.—38 pp. London, H.M.S.O.

DONISTHORPE, H. ST. J. K. (1939). A preliminary list of the Coleoptera of Windsor Forest.—126 pp. London, Nathaniel Lloyd.

DUFFY, E. A. J. (1945). The Coleopterous fauna of the Hants-Surrey border.—Ent. mon. Mag., **81**, pp. 169–179.

FORD, L. T. (1949). A guide to the smaller British Lepidoptera.—230 pp. London, S. Lond. ent. nat. Hist. Soc.

FREEMAN, J. A. (1948*a*). World foci of infestation and principal channels of dissemination to other points, with suggestions for detection and standards of inspection. *In* Easter, S. S. *Ed.* Preservation of grains in storage.—FAO agric. Stud., no. 2, pp. 15–34.

FREEMAN, J. A. (1948*b*). Stored-products pests: a survey of the principal entomological problems in the United Kingdom.—Ann. appl. Biol., **35**, pp. 294–301.

FREEMAN, J. A. & TURTLE, E. E. (1947). Insect pests of food. The control of insects in flour mills.—84 pp. London, Minist. Food.

GARDNER, A. E. (1954). *Blatta orientalis* out-of-doors.—Entomologist, **87**, p. 167.

GOOD, N. E. (1936). The flour beetles of the genus *Tribolium*.—Tech. Bull. U.S. Dep. Agric., no. 498, 58 pp.

HARRISON, G. H. [?1944]. The Woolly Bear with special reference to the species *Anthrenus fasciatus* Herbst.—15 pp., multigraph. [Cawnpore, Ordn. Lab.] (Rev. appl. Ent., (A) **33**, p. 73.)

HERFS, A. (1936). Oekologisch-physiologische Studien an *Anthrenus fasciatus* Herbst.—Zoologica, Stuttgart, **34**, pp. 1–96.

HINTON, H. E. (1941). The Ptinidae of economic importance.—Bull ent. Res., **31**, pp. 331–381.

HINTON, H. E. (1943*a*). *Stethomezium squamosum* gen. et. sp. n. infesting stored food in Britain, with notes on a South African Ptinid not previously recorded in stored products (Coleoptera).—Proc. R. ent. Soc. Lond., (B) **12**, pp. 50–54.

HINTON, H. E. (1943*b*). Notes on two species of *Attagenus* (Col., Dermestidae) recently introduced into Britain.—Ent. mon. Mag., **79**, pp. 224–227.

HINTON, H. E. (1943*c*). A key to the species of *Carpophilus* (Col., Dermestidae) that have been found in Britain, with notes on some species recently introduced with stored food.—Ent. mon. Mag., **79**, pp. 275–277.

HINTON, H. E. (1945). A monograph of the beetles associated with stored products. Volume I.—443 pp. London, Brit. Mus. (Nat. Hist.).

HINTON, H. E. (1948). A synopsis of the genus *Tribolium* Macleay, with some remarks on the evolution of its species-groups (Coleoptera, Tenebrionidae).—Bull. ent. Res., **39**, pp. 13–55.

HOWE, R. (1940). New records of insects in grain stores.—Ent. mon. Mag., **76**, pp. 73–75.

HOWE, R. W. (1949). Studies on beetles of the family Ptinidae. I. Notes on the biology of species in Britain.—Ent. mon. Mag., **85**, pp. 137–139.

HOWE, R. W. (1950). Studies on beetles of the family Ptinidae. III. A two-year study of the distribution and abundance of *Ptinus tectus* Boield. in a warehouse.—Bull. ent. Res., **41**, pp. 371–394.

HOWE, R. W. (1953). *Oryzaephilus mercator* (Fauv.) (Col., Cucujidae), a valid species.—Ent. mon. Mag., **89**, p. 96.

HOWE, R. W. & BURGES, H. D. (1951). Studies on beetles of the family Ptinidae. VI. The biology of *Ptinus fur* (L.) and *P. sexpunctatus* Panzer.—Bull. ent. Res., **42**, pp. 499–511.

HOWE, R. W. & BURGES, H. D. (1952*a*). Studies on beetles of the family Ptinidae. VII. The biology of five Ptinid species found in stored products. —Bull. ent. Res., **43**, pp. 153–186.

HOWE, R. W. & BURGES, H. D. (1952*b*). A note on the survival of *Alphitobius laevigatus* F. (Col., Tenebrionidae) in warm dry conditions.—Ent. mon. Mag., **88**, pp. 160–161.

HOWE, R. W. & BURGES, H. D. (1953*a*). Studies on beetles of the family Ptinidae. 10. The biology of *Mezium affine* Boieldieu.—Ent. mon. Mag., **89**, pp. 217–220.

HOWE, R. W. & BURGES, H. D. (1953*b*). Studies on beetles of the family Ptinidae. IX. A laboratory study of the biology of *Ptinus tectus* Boield. —Bull. ent. Res., **44**, pp. 461–516.

IMMS, A. D. (1937). Recent advances in entomology.—2nd edn., 431 pp. London, Churchill.

JENNINGS, F. B. (1932). *Cathartus advena* Waltl living with Cryptophagi.—Ent. mon. Mag., **68**, p. 231.

JOY, N. H. (1932). A practical handbook of British beetles. Vol. I.—622 pp. London, Witherby.

KIMURA, K. & TAKAKURA, Y. (1919). Researches on controlling insects injurious to dried cod. [In Japanese.]—Suisankoshujo Shiken Hokoku [Exp. Rep. Fish. Inst.] Tokyo, **15**, pp. 1–32. (R.A.E., (A) **8**, p. 255).

KLOET, G. S. & HINCKS, W. D. (1945). A check list of British insects.—483 pp. Stockport. the Authors.

KREYENBERG, J. (1928). Experimentell-biologische Untersuchungen über *Dermestes lardarius* L. und *Dermestes vulpinus* F. Ein Beitrag zur Frage nach der Inkonstanz der Häutungszahlen bei Coleopteren.—Z. angew. Ent., **14**, pp. 140–188. (R.A.E., (A) **16**, p. 657.)

KUNIKE, G. (1939). Beiträge zur Lebensweise und Bekämpfung der Mehlmotte, *Ephestia kuehniella* Z. (Pyralidae, Phycitinae).—Z. angew. Ent., **25**, pp. 588–608. (R.A.E., (A) **27**, p. 399.)

LECLERCQ, J. (1946). Insects brought with the hay from the meadows into the hayloft.—Ent. mon. Mag., **82**, p. 138.

LECLERCQ, J. (1950). Ecologie et physiologie des populations de *Tenebrio molitor* L. (Insecte, Coléoptère).—Physiol. comp., **2**, pp. 161–180.

MALLIS, A. (1945). Handbook of pest control . . .—554 pp. [New York] MacNair-Dorland.

MANLEY, G. (1953). The mean temperature of central England, 1698–1952.—Quart. J. R. met. Soc., **79**, pp. 242–261.

MANSBRIDGE, G. H. (1936). A note on the resistance to prolonged cold of some insect pests of stored products.—Proc. R. ent. Soc. Lond., (A) **11**, pp. 83–86.

MATHLEIN, R. (1938). Undersökningar rörande förrådsskadedjur. I. Kornviveln, *Calandra granaria* L. och risviveln, *Calandra oryzae* L. Deras biologi och bekämpning.—Medd. Växtskyddsanst., no. 23, 91 pp.

MATHLEIN, R. (1943). Undersökningar rörande förrådsskadedjur. III. Svartbruna mjölbaggen, *Tribolium destructor* Uytt. Ett nytt, ekonomiskt viktigt skadedjur.—Medd. Växtskyddsanst., no. 41, 38 pp. (R.A.E., (A) **31**, p. 438.)

MATHLEIN, R. (1944). Ovälkomna invandrare.—Växtskyddsnotiser, **1944**, no. 2, pp. 23–28. (R.A.E., (A) **32**, p. 434.)

MATHLEIN, R. (1948). Ett skadedjur i importerade fodermedel.—Växtskyddsnotiser, **1948**, no. 2, p. 29. (R.A.E., (A) **38**, p. 42.)

MEEUSE, A. D. J. (1950). The Australian Carpet Beetle, *Anthrenocerus australis* (Hope) (Coleoptera, Dermestidae—Anthrenini) in the Netherlands.—Ent. Ber., **13**, pp. 161–162.

MEHL, S. (1940). Die Widerstandsfähigkeit der Raupe der Heumotte (*Ephestia elutella* Hb.) gegen Frost.—Anz. Schädlingsk., **16**, pp. 78–83. (Biol. Abstr., **21**, p. 1241.)

MELLANBY, K. (1939). Low temperature and insect activity.—Proc. roy. Soc., (B) **127**, pp. 473–487.

METEOROLOGICAL OFFICE. Monthly Weather Report.—London, H.M.S.O.

MUNRO, J. W. (1940). Report on a survey of the infestation of grain by insects.—54 pp. London, Dep. sci. industr. Res.

NAGEL, R. H. & SHEPARD, H. H. (1934). The lethal effect of low temperatures on the various stages of the Confused Flour Beetle.—J. agric. Res., **48**, pp. 1009–1016.

O'FARRELL, A. F. & BUTLER, P. M. (1948). Insects and mites associated with the storage and manufacture of foodstuffs in Northern Ireland.—Econ. Proc. R. Dublin Soc., **3**, pp. 343–407.

O'MAHONY, E. (1950). Irish records of introduced Coleoptera.—Ent. mon. Mag., **86**, pp. 72–73.

Oxley, T. A. (1948). The scientific principles of grain storage.—103 pp. Liverpool, Northern Publ. Co.

Payne, N. M. (1934). The differential effect of environmental factors upon *Microbracon hebetor* Say (Hymenoptera: Braconidae) and its host, *Ephestia kühniella* Zeller (Lepidoptera: Pyralidae). II.—Ecol. Monogr., **4**, pp. 1–46.

Powell jr., T. E. (1931). An ecological study of the Tobacco Beetle, *Lasioderma serricorne* Fabr., with special reference to its life history and control.—Ecol. Monogr., **1**, pp. 333–393. (R.A.E., (A) **20**, p. 170.)

Reed, W. D. & Vinzant, J. P. (1942). Control of insects attacking stored tobacco and tobacco products.—Circ. U.S. Dep. Agric., no. 635, 40 pp.

Reitter, Edm. (1911). Fauna Germanica, **3**, 436 pp. Stuttgart, K. G. Lutz.

Richards, O. W. (1944). The two strains of the Rice Weevil, *Calandra oryzae* (L.) (Coleopt., Curculionidae).—Trans. R. ent. Soc. Lond., **94**, pp. 187–200.

Richards, O. W. & Waloff, N. (1946). The study of a population of *Ephestia elutella* Hübner (Lep., Phycitidae) living on bulk grain.—Trans. R. ent. Soc. Lond., **97**, pp. 253–298.

Robinson, W. (1926). Low temperature and moisture as factors in the ecology of the Rice Weevil, *Sitophilus oryzae* L., and the Granary Weevil, *Sitophilus granarius* L.—Tech. Bull. Minn. agric. Exp. Sta., no. 41, 43 pp.

Salt, R. W. (1936). Studies on the freezing process in insects.—Tech. Bull. Minn. agric. Exp. Sta., no. 116, 41 pp.

Salt, R. W. (1950). Time as a factor in the freezing of undercooled insects.—Canad. J. Res., (D) **28**, pp. 285–291.

Salt, R. W. (1953). The influence of food on cold hardiness of insects.—Canad. Ent., **85**, pp. 261–269.

Simmons, P. & Ellington, G. W. (1925). The Ham Beetle, *Necrobia rufipes* de Geer.—J. agric. Res., **30**, pp. 845–863.

Skalov, Yu. Yu. (1931). The biological cycle of the Tobacco Beetle (*Lasioderma serricorne* F.) under the conditions of fermentative factories and the influence of temperature variations on the activity of the insect. [In Russian with German summary.]—Bull. St. Inst. Tobacco Invest., Crimean Sect., Yalta, no. 80, 16 pp. (R.A.E., (A) **21**, p. 196.)

Strong, L. A. (1936). Report of the Chief of the Bureau of Entomology and Plant Quarantine, 1936.—121 pp. Washington, D.C., U.S. Dep. Agric. (R.A.E., (A) **25**, p. 408.)

Swingle, M. C. (1938). Low temperature as a possible means of controlling the Cigarette Beetle in stored tobacco.—Circ. U.S. Dep. Agric., no. 462, 8 pp. (R.A.E., (A) **26**, p. 363.)

Takio, M. (1937). Morphology and ecology of *Dermestes vorax* Motsch. [*In Japanese.*]—Bull. seric. Exp. Sta. Japan, **9**, pp. 167–184. (R.A.E., (A) **26**, p. 515.)

Tenhet, J. N. & Bare, C. O. (1951). Cold storage to control the Cigarette Beetle in cigar tobaccos.—U.S. Dep. Agric. Bur. Ent., E-827, 8 pp. multigraph.

Thomas, E. L. & Shepard, H. H. (1940). The influence of temperature, moisture, and food upon the development and survival of the Saw-toothed Grain Beetle.—J. agric. Res., **60**, pp. 605–615.

USHATINSKAYA, R. S. (1948). The importance of sudden and gradual falls of temperature on the "cold stability" of the Granary Weevil (*Calandra granaria* L.). [*In Russian.*]—Zool. Zh., **27**, pp. 495–502.

USHATINSKAYA, R. S. (1950*a*). Resistance to cold of grain weevils *Calandra granaria* and *Sitophilus oryzae*. [*In Russian.*]—Bull. Acad. Sci. U.R.S.S., (Biol.) **1950**, pp. 17–28.

USHATINSKAYA, R. S. (1950*b*). The influence of the humidity of the surroundings and of food on the cold resistance of the Granary Weevil, *Calandra granaria*. [*In Russian.*]—Zool. Zh., **29**, pp. 341–349.

VERDCOURT, B. (1948). The habitat of *Alphitophagus bifasciatus* Say, etc. (Col.. Tenebrionidae).—Ent. mon. Mag., **84**, p. 98.

VOELKEL, H. (1924). Zur Biologie und Bekämpfung des Khaprakäfers, *Trogoderma granarium* Everts.—Arb. biol. Reichsanst. Land- u. Forstw., **13**, pp. 129–171.

WALKER, J. J. (1907). A preliminary list of the Coleoptera of the Oxford district. —Rep. Ashmol. nat. Hist. Soc., 1906, pp. 51–99.

WALOFF, N. (1949). Observations on larvae of *Ephestia elutella* Hübner (Lep. Phycitidae) during diapause.—Trans. R. ent. Soc. Lond., **100**, pp. 147–159.

WIGGLESWORTH, V. B. (1950). The principles of insect physiology.—4th edn., 544 pp. London, Methuen.

WILLIAMS, G. C. (1954). Observations on the effect of exposure to a low temperature on *Laemophloeus minutus* (Ol.) (Col. Cucujidae).—Bull. ent. Res., **45**, pp. 351–359.

WOODROFFE, G. E. (1950). The identity of the Case-bearing Clothes Moth (Lep., Tinaeidae).—Ent. mon. Mag., **86**, p. 181.

WOODROFFE, G. E. (1953). An ecological study of the insects and mites in the nests of certain birds in Britain.—Bull. ent. Res., **44**, pp. 739–772.

WOODROFFE, G. E. & SOUTHGATE, B. J. (1951). Birds' nests as a source of domestic pests.—Proc. zool. Soc. Lond., **121**, pp. 55–62.

ZACHER, F. (1939). Verschleppung und Einbürgerung von Vorratsschädlingen. —Verh. VII. int. Kongr. Ent., **4**, pp. 2919–2926.

ZACHER, F. (1944). Vorratsschutz gegen Schädlinge.—113 pp. Berlin, Parey.

ZINKERNAGEL, R. (1952). Remarks on *Attagenus* species.—Trans. IXth int. Congr. Ent., **1**, pp. 844–848.

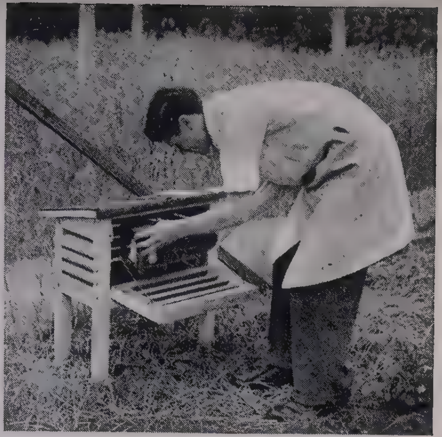


FIG. 1. Small screen.

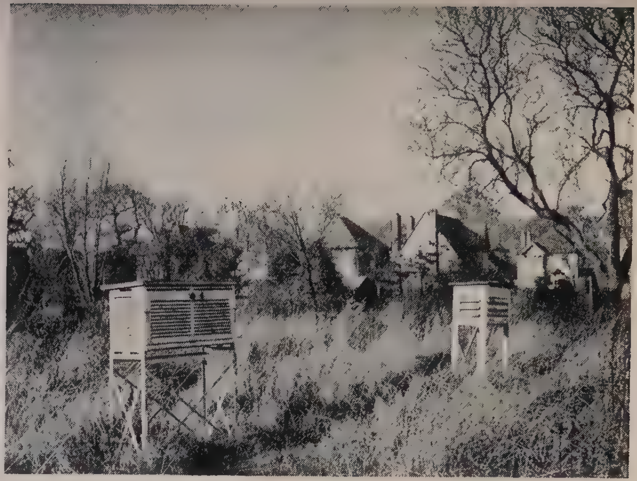


FIG. 2. Stevenson screen and (on right) heavier screen of same size.

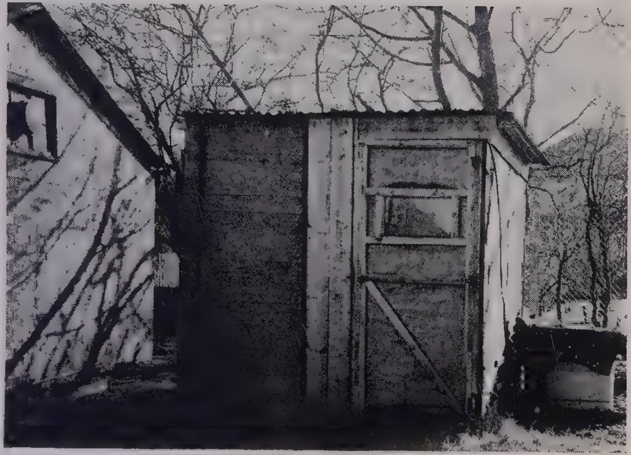


FIG. 3. Fly Hut.

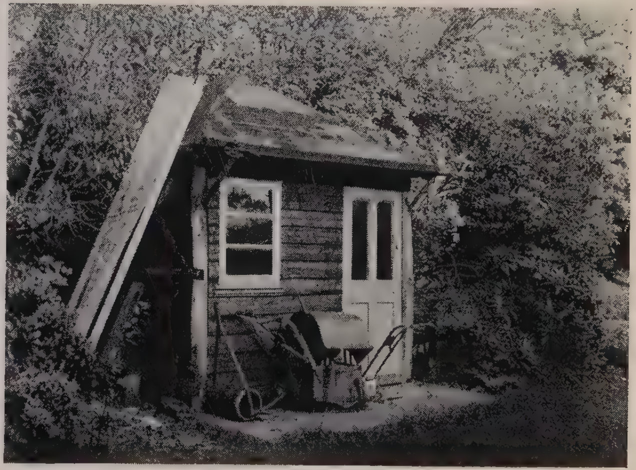


FIG. 4. Summer-house.

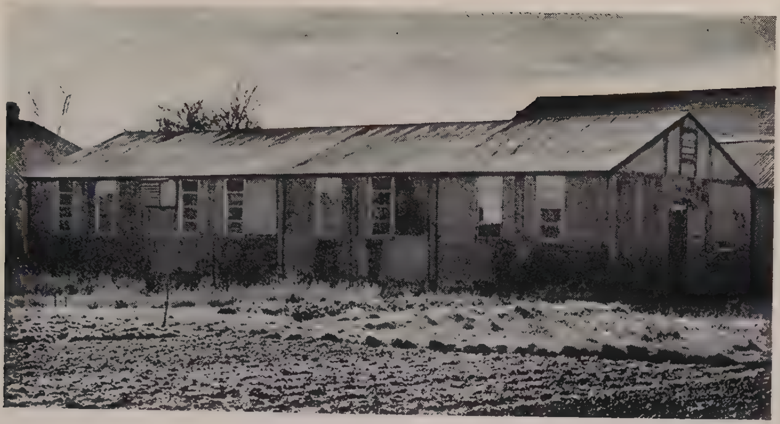


FIG. 1. Hut 49.

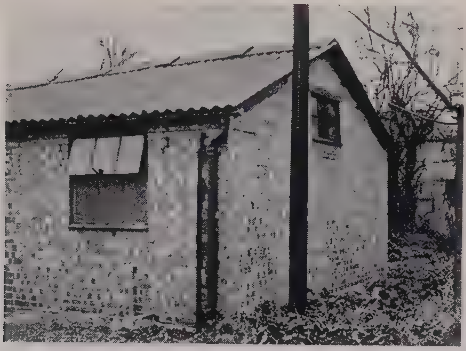


FIG. 2. Mansbridge's Hut.

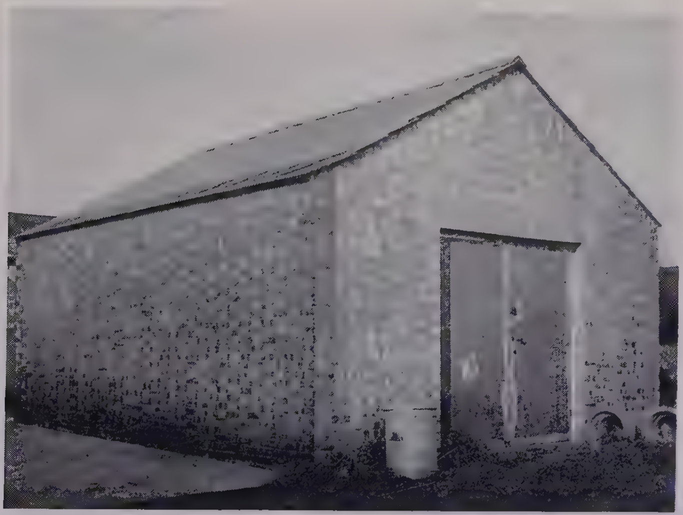


FIG. 3. Grain Store.

THE FERTILISATION OF *GLOSSINA PALPALIS* IN CAPTIVITY.

By T. A. M. Nash, O.B.E., D.Sc.

Deputy Director, West African Institute for Trypanosomiasis Research,
Kaduna, N. Nigeria.

An important function of the Entomological Section of this Institute is to breed large numbers of clean *Glossina palpalis* (R.-D.) for the Institute's research and for workers in other countries.

We originally adopted in detail the technique described by Professor Geigy (1948). In his method, 14 newly emerged tsetse flies, six males and eight females, are placed in a small cage and are kept together for the rest of their lives. Since our results were poor, the reproduction rate being very low, we suspected that poor fertilisation might be one of the causes. Dissection of 45 females, 15 days old, and examination of the spermathecae showed that 27 per cent. were unfertilised. Admittedly, in view of subsequent research, the number dissected was too low to give a reliable result, but at the time no more flies could be spared.

We then tried a variety of methods based on putting the sexes together in large mating cages, when the individuals of each sex had reached the most suitable age, as determined by Mellanby (1936) in Uganda. Results continued to be unsatisfactory, suggesting that further research on fertilisation was required.

Before describing such research it should be mentioned that newly emerged flies are collected daily at 9 a.m. and are then taken to be one day old—a convention that it is believed Mellanby and others have followed. In point of fact such flies may be anything from 0–24 hours old, but since about three-quarters of the emergence takes place before dusk on the previous day it follows that 75 per cent. of the flies are 14–24 hours old. Undoubtedly, it would be more accurate to refer to flies as being $\frac{3}{4}$, $1\frac{3}{4}$, $2\frac{3}{4}$ . . . . $9\frac{3}{4}$ days old when mated, but for the sake of convenience they will be referred to throughout this paper as 1, 2, 3 . . . . 10 days old.

The mating cages referred to are 12 × 13 × 13 inches in size, and consist of a wooden framework fitted with a glass top for observation, mosquito-netting sides and a cloth bottom. They hold comfortably about 100 tsetse.

The Age at which young Males become virile.

Mellanby (1936) found that " no males under 5 days old fertilised any females, but those 6 days and older were fully potent ". He does not mention the number of flies on which these observations were based.

The first part of his finding does not hold good in Nigeria. It is not unusual to find that when the sexes are separated within 24 hours of emergence a few females will produce perfectly normal larvae, indicating that successful fertilisation must have taken place shortly after emergence. Dissection and spermathecal examination of 532 females that had been segregated within 24 hours of emergence showed that 3·8 per cent. were fertilised. Under such conditions, fertilisation can take place, but at a very low rate; clearly a few males under 24 hours old must be potent.

Shortage of stock prohibited the mating of females with males of different ages and the study of the effectiveness of fertilisation by spermathecal examination. The following, less satisfactory, method was devised which obviated the need to destroy females.

Observations were made on the relative virility shown by young males, marked white, when forced to compete for the females' favours with an equal number of older males marked red. Five mating cages were used for the five batches of young, white males which were aged as follows:—2, 3, 4, 5–6 and 7–8 days old. The older red males were of mixed ages, ranging from 9 to 33 days. The sex proportion employed was two males, one white and one red, to each female.

Observations were taken at the following intervals after the sexes had been placed together—¼ to ½ hour, 1½, 2½, 3½, 6½, 20½, 23½ and 44½ hours. At the time of each observation four separate counts were made of the total number of copulations in each cage and the colour of the males responsible; the average figure for these counts was recorded. It was not unusual in the first observation to find that the number of copulations by young white males decreased from count to count, as the old males knocked them off the females. When this happens, it is most improbable that the young males succeed in fertilising the females, for Mellanby has shown, and the writer has since confirmed, that the sperm does not pass until just before the flies separate of their own volition, which is usually a matter of one or two hours. Owing to this long duration of mating, the same pair may have been recorded in two consecutive observations.

The results are given in Table I. Larger numbers of flies were used in cages IV and V, because Mellanby's findings suggested that any changes in virility would be most likely to occur among males 5 to 8 days old. It was impossible to use females of the same age for all cages, but even though females are more attractive at certain ages than others, this will not affect the present investigation, where the *relative* virility of young and old males, confronted in the same cage with the same conditions, is being studied.

The last column of Table I indicates that the virility of young males, under 7 days old, is far less than that of older males, aged from 9 to 33 days. Since these results on virility tend to confirm Mellanby's results on potency, no flies are added to our stock of stud males until they are one week old.

The Time required to mate a Batch of Females.

A series of experiments was undertaken, using old males, and females of different ages, in which it was hoped to ascertain the age at which the female

TABLE I.

The age at which the virility of young males approaches that of older males when competing for females.

Cage No.	Age in days of young males	No. of females in cage	Age in days of females	Total matings observed	Percentage of total matings effected by young males
I	2	18	4	14	0
II	3	33	2	51	14
III	4	33	3	56	11
IV	5–6	50	5–6	51	18
V	7–8	50	7–8	49	39
Total		184		221	

was most attractive, by comparing the "matings per female figure" for the various mating cages. The results suggested that females 6–8 days old were far less attractive than those that were 1–5 days old, and that of the latter, those 3 days old were possibly the most attractive. Since this subject was later investigated by the much more accurate method of spermathecal examination, the results will not be given, but out of this series of experiments some interesting information was obtained as to how long it is necessary to leave the sexes together to obtain maximal fertilisation.

Males were always supplied in excess of the number of females, the sex ratio being 57 males to 43 females. Both sexes were always given an opportunity of feeding before being placed in the mating cages. In this series of experiments 1,042 females were used.

TABLE II.

The incidence of copulation during the first 23 hours after the sexes are put together.

Time of observation	Copulations counted	Incidence, as percentage of total copulations
¼ to ½ hour	371	29·4
1½ hours	277	22·0
2½ ,,	254	20·2
3½ ,,	230	18·2
6 ,,	93	7·4
20 ,,	32	2·5
23 ,,	4	0·3
Total	1,261	100·0

Based on consolidated data from a series of observations made at fixed intervals on a total of 1,042 females and 1,380 males.

It is clear from Table II that copulations are most numerous shortly after the sexes are put together, but decrease steadily, becoming only a quarter as numerous six hours later. Next morning, after 20 hours, there are very few matings, and after 23 hours, copulation has virtually ceased, although males still make abortive attacks on the females. The flies used to be left in the mating cages for 48 hours, but now are removed after only one day.

It is worth recording the typical behaviour of virile males when first added to a mating cage containing females of an attractive age. As the males are shaken out of their containers, pairs start appearing on the walls, but with such speed that the eye cannot see how it comes about. In some cases, however, a short, sharp struggle takes place before the female accepts the male. If the females are highly attractive and willing, 60 per cent. of them may have paired by the time the last male is shaken out.

The cessation of copulation after 23 hours could be due to sexual exhaustion on the part of the male or to loss of attractiveness by the female, but the abortive attacks made by the males even at the end of the period suggest that neither explanation is correct. The point was elucidated by adding a new batch of virile males at the end of 23 hours.

Forty-three females, 3 days old, had been mated with 86 old males. Observations 20, 21, 22 and 23 hours after the sexes had first been put together showed only 3, 0, 0 and 1 pair, respectively; mating had virtually ceased. The females, now 4 days old—an attractive age, as will be shown later—were transferred to a new cage, and 57 virgin males, 8 days old, were added. There was no doubt about their ardour or that the females were still attractive. On release, the males dived at the females, and there were many struggling pairs tumbling about on the floor of the cage, but within seconds the females managed to free themselves. Counts made ¼ to ½ hour after the sexes had been put together revealed only one pair in copulation, although the fresh males were still making abortive efforts to mate. Yet it was known from the previous results on 11 mating cages containing 43 per cent. *virgin* females four days old and 57 per cent. old males, that the expected number of pairs at the time of the first observations should have ranged from 24 to 42 per cent. of the females available, the average being 33 per cent.; whereas 14 pairs might have been expected, there was only one. Clearly, females are still attractive after being kept for 23 hours with an excess of males, but they cease to be *willing* to pair and are able to repulse the male—an ability also described by Squire (1951).

Since this unwillingness might have been due to hunger, 23 hours having elapsed since the females last had a chance to feed, the above experiment was repeated in every detail except that this time the females were given 15 minutes in which to feed before being subjected to the attentions of a new batch of males. Again, many struggling pairs appeared on the floor, but this time a number of females were compliant. Counts made ¼ to ½ hour after the males had been added revealed 7 pairs, *i.e.*, 16 per cent. of the females had mated.

Clearly, the unwillingness of the female to pair, after spending 23 hours with an excess of males, can be largely overcome by feeding her.

The Age at which Females are most readily fertilised.

Mellanby (1936) placed females of known age in a cage with twice their number of 8-day-old potent males. He records that "dissection after 24 hours showed that among females aged 1–4 days, only between 20 and 40 per cent. were fertilised. In flies of 5 to 8 days old, an average of 75–90 per cent. was reached. Females older than 8 days became less attractive again." No indication is given of the number of observations upon which these conclusions are based.

As mentioned in the last section, the writer's preliminary results, based on copulation counts at fixed intervals, suggested very different results, namely, that females 1–5 days old are much more willing to copulate than those 6–8 days old.

Squire (1952) found that, in the field, the absence of mating scars is almost confined to the newly emerged, teneral flies, which he defines as those flies with a thorax that feels soft and yielding when held between the thumb and index finger. He concludes that the teneral stage is the mating phase *par excellence*, and estimates that this stage ends about seven days after emergence.

As the existing information was contradictory, it was decided to repeat Mellanby's experiment on a large scale.

The attractiveness of females from 1 to 10 days old was investigated. On achieving the desired age, the females were placed with twice their number of potent, virgin males which were 7 or 8 days old; occasionally, the numbers had to be made up with a few older males. After 24 hours, the females were chloroformed, dissected, and the spermathecae examined by the writer. It is important to examine the spermathecae as soon as the dissection is made, as sometimes the contents will leak out of the severed ends of the ducts.

If both the spermathecae are completely transparent, when examined by natural reflected light under a binocular microscope with a x50 magnification, then the fly is classed as virgin, and the degree of impregnation is recorded as 0·00 + 0·00 = 0·00. Not uncommonly one or both vesicles are indented on their contiguous faces; care should be taken that the opacity, due to the four layers of chitin forming the fold, is not mistaken for spermathecal content. The empty spermathecae of a virgin fly are usually a golden honey colour, but in some cases they may be much darker and occasionally so dark that artificial light has to be used before one can be certain that they are really empty. Sometimes a very small opaque blob may be seen in the centre of one vesicle, and in such cases the fly should be counted as fertilised, as females in this condition have been found to contain a larva.

If a female is fully impregnated both vesicles are dark brown and completely opaque; this degree of impregnation is expressed as 1·00 + 1·00 = 2·00.

Many females are fertilised but only partially impregnated. One vesicle may be full and the other empty, or one half-full and the other one-quarter full; in such cases the degree of impregnation is recorded as 1·00 + 0·00 = 1·00, and 0·50 + 0·25 = 0·75, respectively. Mellanby (1936) gives an illustration of partially impregnated spermathecae in which the opaque area occupies the proximal part of the vesicle adjacent to the duct. This is the normal picture for older females, but the writer has found that with recently fertilised and only partially impregnated flies, the opaque area is either distal or takes the form of a central opacity surrounded by a golden transparent halo. Presumably it takes some time for the sperm to settle down into a mass near the mouth of the duct.

The average impregnation figure was worked out for the fertilised females in each batch, and will be referred to as the " spermathecal value ". It seemed possible that although the fertilisation rate might be similar for batches of females of different ages, yet the impregnation rate might be far lower if at one age the females copulated with reluctance. In such a case, the degree of impregnation might prove inadequate to keep the female fertilised throughout her life.

Altogether 900 females were dissected in this experiment, 90 for each of the ten ages studied.

The total of 90 flies used for each age was composed of four separate matings and dissections of 22, 20, 20 and 28 females, respectively, spread over a period of three months; hence the final figure was based on a fair random sample. The matings all took place on the same bench in the fly room, where the climate is controlled, the temperature ranging from 78–81°F. (25·6–27·2°C.) with a relative humidity around 75 per cent.

TABLE III.

The age at which the female of *G. palpalis* is most readily fertilised.

Age of females at start of mating	Total dissected 24 hours later	Total virgins	Total fertilised	Percentage fertilised	Mean spermathecal value for fertilised females
1 day	90	23	67	74·4	1·8
2 days	90	32	58	64·4	1·8
3 days	90	14	76	84·4	1·9
4 days	90	22	68	75·6	1·8
5 days	90	21	69	76·6	1·9
6 days	90	26	64	71·1	1·8
7 days	90	28	62	68·9	1·9
8 days	90	27	63	70·0	1·8
9 days	90	36	54	60·0	1·8
10 days	90	31	59	65·6	1·8

Males all virgin and 7 or 8 days old. Two males available for each female, and sexes kept together for 24 hours.

The results are given in Table III, but the percentage fertilisation obtained with females of different ages is also shown graphically in fig. 1. Inspection of this figure indicates that with females of any age from 1–10 days at least 60 per cent. will become fertilised, and that there can be no suggestion that females even as young as 1 day old or less are not readily fertilised. It may be noted that the very poor fertilisations observed among females which had been segregated from males within 24 hours of emergence, must clearly be due solely to lack of potency in very young males. If the graph is examined in more detail it will be noticed that over the first five days fertilisation is good, apart from the second day, and is exceptionally good for the third day. From the sixth to the eighth day, fertilisation is at a lower rate, and for the ninth and tenth days it is relatively bad.

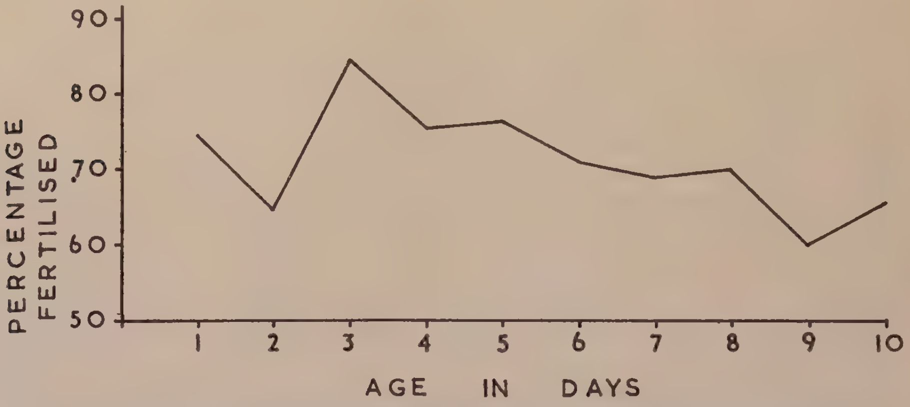


Fig. 1.—The fertilisation percentage obtained with females of different ages, when left for 24 hours with twice as many virgin males 7–8 days old.

I am deeply indebted to Dr. D. Gall, Research Epidemiologist of this Institute, for his kindness in submitting the data given in Table III to statistical analysis, with the following results.

Comparing the fertilisation rates obtained in the first 10 days, we find that only the 3-day-old female flies show a performance which is substantially above the average, and this differs significantly from that of the other nine ages when tested for independence ($\chi^2 = 8{\cdot}654$, $P < 0{\cdot}01$).

Comparing the fertilisation rate over the first five days with that over the second five days, a significantly lower rate is found in the latter ($\chi^2 = 7{\cdot}010$, $P < 0{\cdot}01$). The resultant lowering of the average over the whole ten days tends to mask the poor performance of 2-day-old flies. When compared with the average of 1-, 3-, 4- and 5-day-old flies only, the performance of 2-day-old flies is found to be significantly lower ($\chi^2 = 6{\cdot}847$, $P < 0{\cdot}01$).

No explanation can be given for the poor performance of the 2-day-old females, but the results for the four batches making up the 90 females dissected were consistently low and remarkably steady being 64, 65, 65 and 64 per cent. fertilised.

The writer's findings differ most strikingly from those of Mellanby (1936) who obtained a 20–40 per cent. fertilisation with females 1–4 days old, but a 75–90 per cent. fertilisation with females 5–8 days old. Either the Uganda race of *G. palpalis* behaves entirely differently from the Nigerian race, or Mellanby's results were based on too small numbers. In this connection it should be mentioned that a considerable variation was often found in the fertilisation rate of batches of about 20 flies of the same age. It was not until some 60 flies had been dissected for each age that the final picture started to emerge.

The degree of impregnation among the fertilised females is uniformly high at all ages, ranging from 1·8 to 1·9 (Table III, last column). A mean spermathecal value of 2·0 could only have been achieved had every female been fully impregnated; 75 per cent. of the 3-day-old females were fully impregnated.

The Application of these Results to the large-scale Breeding of *G. palpalis*.

As a result of these findings we have been mating all females on their third day of life with twice as many males, none of them under 7 days old. After mating, the females are housed at the rate of 20 per Bruce box. Five young males are also added to each box on the principle that they may succeed in fertilising some of the females that escape impregnation in the mating cages, and that they may be of value in re-fertilising old females that may have used up their store of sperm.

Samples of the females were taken from the breeding cupboards to ascertain the fertilisation rate achieved under normal conditions of routine maintenance. Samples were also taken from females that had been mated in the proportion of 43 per cent. females and 57 per cent. males instead of the usual proportion of 33 per cent. females and 67 per cent. males, as occasionally, owing to a scarcity of stud males, it is necessary to use them at the lower figure.

Over a period of three months, eight samples, each of 50 females, were removed for dissection on the 16th day of the female's life. Four of these samples consisted of females that had been mated with the normal 67 per cent. males, and four of females that had been mated with only 57 per cent. males. The results are given in Table IV.

TABLE IV.

The fertilisation rate achieved in the fly room, as found by random samples.

Males per cent. at mating	Total females dissected	Number fertilised	Percentage fertilised	Mean spermathecal value	No. 3rd-stage larvae *in situ*	No. of pupae already produced
67	200	177	88·5	1·5	74	33
57	200	175	87·5	1·5	59	15

All males over 6 days old. Virgin females mated on 3rd day of life for 24 hours, and then housed in Bruce boxes at the rate of 20 females to 5 young males. Females dissected on 16th day of life.

There is no appreciable difference in the percentage fertilised between females that had been mated with 67 or 57 per cent. males. The average proportion fertilised among the 400 females dissected can be taken as 88 per cent. Out of 5,545 wild females dissected the fertilisation rate was 96 per cent. (Nash & Page, 1953), so that fertilisation amongst our captive flies is now only 8 per cent. less than that found in the field. For the eight samples of 50 females that were dissected the fertilisation rates obtained were 96, 96, 94, 92, 84, 82, 82, and 78 per cent. Clearly, fertilisation can be as good as that found in the field, but for some unknown reason it is low in certain batches. Possibly in these cases the females fed badly before being put in the mating cages, so in future the feeding time for such flies is being increased from 15 to 30 minutes.

When breeding tsetse on a large scale the biggest item of expense is their feeding. When running a colony of 4,000 supposedly fertilised females, if in reality only 73 per cent. are fertilised then 1,080 useless females are being fed daily; now, having raised the figure to 88 per cent., only 480 such females are being kept.

Whether there is any advantage to be gained by adding 5 young males to each Bruce box is not yet proven, but the percentage fertilised in Table IV is 4 per cent. higher than the figure obtained for 3-day-old females dissected after 24 hours (Table III).

In the last two columns of Table IV, figures are given for the number of third-stage larvae found when dissecting the females on their 16th day of life and for any pupae which they may have already produced. The poorer showing for those flies mated with 57 per cent. males is of no significance, and is almost entirely due to the first batch of 50, which owing to an unavoidable drop in the fly-room temperature had barely started to produce before dissection. It will be seen from the 67 per cent. group that by the 16th day of life 107 of the 200 females had already produced or were just about to produce pupae.

Turning now to the fifth column of Table IV, the mean spermathecal value 13 days after fertilisation is only 1·5, whereas for flies mated at a similar age and dissected one day after fertilisation it was 1·9 (Table III). This difference may be due to the fact that under routine maintenance conditions the old males used for mating are not virgins and therefore may often be incapable of providing maximal impregnation, or to a normal decrease in the spermathecal content as the females age.

The Re-fertilisation and Reproductivity of old Females.

Little seems to be known about whether re-fertilisation is necessary for *some* of the very old females, and if so whether it can take place.

Mellanby (1936) records that the spermathecae of one female were still full of living sperm 200 days after fertilisation. On the other hand Squire (1951) found that as many as 5 per cent. of wild females from his oldest age group, although bearing mating scars, had empty spermathecae; he believes that renewed mating later in life is necessary in some cases, but his data are scanty.

The writer has tried examining the spermathecae of very old females, but had to discard his figures owing to the number of doubtful cases in which the vesicles are very dark brown and neither opaque nor transparent, but translucent. He cannot decide whether these are virgins whose spermathecal walls have become darkened and thickened with age, or fertilised females whose spermathecae have become empty. Nor has he managed to convince himself that active sperm can be seen under the microscope by rupturing the spermathecae. Admittedly under phase contrast a violent movement is discernible, but such movement is also discernible in ruptured spermathecae from known virgin flies. Dr. Gall, a pathologist, is convinced that it is Brownian movement. However, no serious attempt has been made to investigate the subject, and Mellanby (1936) and Squire (1951) may well be right in saying that active sperm can be seen.

With regard to whether old females are attractive to males and willing to mate, the writer carried out three small experiments based on copulation counts.

Experiment 1.

Sixteen females known to be from 65–71 days old were placed in a mating cage to which were added 21 virgin males 7 days old, *i.e.*, 57 per cent. male proportion. On first adding the males, a few tentative copulations were observed, but ¼ hour and 1 hour later there were no pairs.

Experiment 2.

Twenty females, at least 73 days old, were placed in a mating cage with a 57 per cent. proportion of old males. There was much scrambling and the females showed considerable resistance, but ¼ hour after the sexes were placed together there were 4 pairs, as there were after ½ an hour, but by an hour there were no pairs. Nevertheless, it is probable that 20 per cent. of the females present were re-fertilised.

Experiment 3.

Thirteen females, about 123 days old, were placed with 26 virile males for 24 hours, but no copulations were seen. The males appeared to be completely disinterested in the females.

The results are very variable, but show that old females can sometimes be attractive to males, and that a few are willing to pair. It was shown in Table III that when dealing with virgin females 1–10 days old, fertilisation was highest amongst those that were 3 days old and thereafter tended to decrease; had the experiment been continued beyond 10 days there might have been other peak periods. Similarly, it is conceivable that there are definite periods throughout the life of the fertilised female when she is attractive and willing to be re-fertilised.

Evidence has been collected which suggests that the reproductivity of the female decreases with age. The monthly reproduction rate in the fly room is expressed as pupae per female per month (P.F.M.), the figure being derived from the month's total pupal production divided by the average fertilised female stock for the first twenty days of that month; stock added over the last 10 days is ignored because it could not have contributed to the pupal production.* In June 1953 we found that one of the goats used for fly-feeding was infected with trypanosomes and that therefore our flies were infected. All adult stock was removed to a separate building called the " goat house ". The fly room was then gradually re-stocked with clean flies that had just emerged from pupae. Hence the goat house started with a mixed fly population of all ages, the mean age of which rapidly rose because no young flies were added, whilst the fly room was re-stocked entirely with young flies, so that in the initial stages the population consisted entirely of young individuals.

The monthly reproduction rates for the two breeding establishments are given in Table V.

It will be seen that as the average age of the goat-house fly population rapidly increased, so the reproduction rate rapidly decreased, from 1·36 to 0·41

TABLE V.

Monthly reproduction rates (pupae per female per month) for an old and young population, respectively.

Month	Goat house		Fly room	
	Av. stock	P.F.M.	Av. stock	P.F.M.
July 1953	767	1·36	360	2·33
Aug. ,,	384	1·00	1,297	2·00
Sept. ,,	133	0·90	2,620	1·63
Oct. ,,	17	0·41	3,404	1·55
Nov. ,,	—	—	3,500	1·38
Dec. ,,	—	—	3,826	1·28
Jan. 1954	—	—	3,904	1·24
Feb. ,,	—	—	3,679	1·25

---

* In the case of the goat-house and wild-fly-breeding establishments mentioned later, the figure for average stock is based on the whole month.

P.F.M. in four months. The normal range is from 1·7 to 1·1. By contrast, in the fly room, record reproduction rates were obtained for the first two months, by the end of which time the oldest female was only 66 days of age. Admittedly, the reproduction rate also fell here as the average age of the population increased, but it fell from an abnormally high figure down to the normal, not from the normal down to a record low figure, as in the goat house.

A few individuals from the first batch of 400 females used to re-stock the fly room lived for 192 to 212 days; hence any effect of increasing average age upon the reproduction rate would not nominally have been completed until mid-January. In practice, such very old individuals, even if all barren, would be too few in numbers to lower the reproduction rate appreciably, but it is quite possible that such an effect was operative until the end of November, after which the P.F.M. figure became steady.

The reproduction rate amongst wild *G. palpalis* brought in from the bush and kept in a separate establishment had been consistently higher than that of the fly room for the 31 months prior to July 1953—the best figure had been 2·63 P.F.M. as against 1·70 P.F.M. for the fly room. But in July, when no female in the fly-room stock was over 36 days old, the reproduction rate was 2·33 P.F.M., a figure that was identical, as it happened, with that obtained from an average stock of 916 wild females; in August the comparable figures for the two establishments were 2·00 and 2·65 P.F.M. respectively. It is a remarkable fact that the only two months in which laboratory-bred flies have approached the high wild-fly reproduction rate have been those in which the mean age of the fly-room stock has been abnormally low, with no female more than 66 days old. Instead of there being something radically wrong with our breeding technique, can it be that the secret is to discard all old females? Possibly wild flies do not survive captivity as well as laboratory-bred flies and therefore relatively few females achieve old age. If this is the case a colony of captive wild flies would have a much lower mean age.

An experiment using 800 females has now shown that reproduction does decrease with age. The reproduction rate per thirty-day period, starting from when the first pupae were deposited, gave the following results, expressed as pupae per female per month:— 0–30 days, 2·1; 31–60 days, 1·4; 61–90 days, 1·2; 91–120 days, 1·09.

Since pupal deposition starts on about the fifteenth day of life, 15 days should be added to these periods to get the approximate age in days of the females, which were thus 15–45, 46–75, 76–105 and 106–135.

A similar experiment has been started at a much more favourable season (June), as under such conditions very high reproduction rates may extend from 0–60 days and not only from 0–30 days.

Summary.

In breeding *Glossina palpalis* (R.-D.) in captivity in Northern Nigeria, it was found that even though the sexes are segregated within 24 hours of emergence, a few females succeed in producing larvae. Examination of the spermathecae of females thus segregated shows that nearly 4 per cent. are fertilised. This low fertilisation rate is due to the impotence of most males under 24 hours old. When young males of different ages were forced to compete with older males for the females' favours, it was found that young males must be 7 to 8 days old before their virility approaches that of older males.

When virile males are added to mating cages containing virgin females, pairing starts immediately, but the number of pairs decreases steadily until after 23 hours, pairing has virtually ceased. The cessation of copulation is due to the female becoming unwilling to pair and to her ability to repulse the male; but if she is re-fed her willingness will be restored to a considerable extent. There

is no need to leave the sexes together for more than 24 hours, as excellent fertilisation can be achieved in that time.

A study was made of the age at which females are most readily fertilised when placed for 24 hours with twice their own number of virgin males 7–8 days old. As a result of 900 spermathecal examinations, the following conclusions were reached:

(a) Fertilisation is significantly greatest among females that are three days old; at this age 84 per cent. became fertilised.

(b) Two-day-old females are singularly difficult to fertilise, but even so, as a group, females 1–5 days old are more readily fertilised than those 6–10 days old. The results are statistically significant.

(c) The average degree of impregnation among fertilised flies is very similar for all ages investigated.

The routine method now employed in the fly room consists in placing 3-day-old females in a mating cage with old males in the proportion of 33 females to 67 males, or sometimes 43 females to 57 males. After 24 hours the females are taken out and then housed at the rate of 20 females and 5 young males to each Bruce box. Over a period of three months, 8 samples each of 50 females were removed on the 16th day of life and dissected, as a check on the fertilisation rate being achieved; the following results were obtained:

(a) Out of 400 females dissected, 88 per cent. were fertilised; this is only 8 per cent. less than in the field.

(b) It seems to make little difference whether the females are mated with a 67 or 57 per cent. proportion of males.

(c) The value of adding 5 young males to each Bruce box is not proven, but it may increase the fertilisation rate, and permits the re-fertilisation of old females, which may be necessary in some cases.

The attractiveness to males of old females, and their willingness to be re-fertilised, is very variable. In one case, females 65–71 days old were attractive but unwilling; in another case, females at least 73 days old were attractive and fairly willing, but in a third case, females about 123 days old were not even attractive.

Evidence has been collected which suggests that the reproductivity of the female decreases considerably with age. It might therefore be advisable in tsetse breeding establishments to destroy the older females and get a quick turn-over of young, highly productive flies.

Acknowledgements.

I am greatly indebted to Mallam H. M. Yesufu, Technical Assistant, who was responsible for organising that tsetse from the fly room were mated, or available for dissection, at the required ages. Acknowledgements are also due to Mr. J. A. Roberts, Laboratory Superintendent, who looks after the fly room, for working out the statistical calculations under Dr. Gall's guidance. Mr. G. M. F. Juldeh and Mr. Christopher Eke carried out the dissections most competently.

References.

Geigy, R. (1948). Elevage de *Glossina palpalis.*—Acta trop., Basel **5**, pp. 201–218.

Mellanby, K. (1936). Experimental work with the tsetse-fly, *Glossina palpalis*, in Uganda.—Bull. ent. Res., **27**, pp. 611–632.

Nash, T. A. M. & Page, W. A. (1953). The ecology of *Glossina palpalis* in Northern Nigeria.—Trans. R. ent. Soc. Lond., **104**, pp. 71–169.

Squire, F. A. (1951). Observations on mating scars in *Glossina palpalis* (R.-D.).—Bull. ent. Res., **42**, pp. 601–604.

Squire, F. A. (1952). On the sex ratio in *Glossina*.—Bull. ent. Res., **43** pp. 231–235.

POPULATION STUDIES OF THE PEA APHID IN EAST ANGLIA.

By J. A. Dunn and D. W. Wright

National Vegetable Research Station, Wellesbourne, Warwick.

E.M.N.

Whilst studying the biology of the Pea Aphid, *Acyrthosiphon pisum* (Harris) in East Anglia, information has been obtained between 1948 and 1951 on the annual population fluctuations of this insect. Population data have been drawn from several leguminous crops which are important hosts of the Pea Aphid.

The most extensive studies have been made on lucerne, *Medicago sativa.* Consecutive data have also been obtained from hop trefoil, *Medicago lupulina,* but these have been less comprehensive owing to the shorter seasonal duration of this biennial crop. Populations of the Pea Aphid have also been followed on sainfoin, *Onobrychis sativa,* and on peas.

During the winter of 1950–51, a series of counts of Pea Aphid eggs was made on both a field of lucerne and of hop trefoil, and the data will be given in another paper.

Sampling Methods used.

The sweeping method.

The majority of crops which support Pea Aphids present a continuous carpet of foliage which can be readily sampled by sweeping.

All the sweeping samples taken during the population studies were obtained in the same standard fashion. A 12-inch sweeping net was used, this being supported on a handle, 2 ft. 6 in. long, which was held at arm's length. Twenty-five semi-circular sweeps went to each sample, which was subdivided, during the taking, into five sets of five sweeps, each of these sets being separated by ten paces and each sweep in the five sets by two paces. The sweeping was carried out, at approximately weekly intervals, by the same person in all except a few unavoidable cases. This minimised discrepancies arising from variations in sampling technique between individuals.

An area of about an acre, where the plants were most uniform in number and growth, was selected within a field for periodic sweeping. The area was also free from weeds and this ensured that the Aphids taken in the samples were, with no recorded exceptions, all Pea Aphids. After each set of five sweeps had been taken, the sweeping net was emptied into a paper bag. Each bag was injected with ½–1 cc. of methyl iso-butyl ketone and was then put into an airtight container. The amount of fumigant used was just sufficient to kill both Aphids and predators and to keep them in a relaxed condition without causing discoloration.

Throughout the summer, the Aphids in each sample were separated into mature winged, immature winged, mature wingless, immature wingless.

In autumn, when the sexual generation appeared, the mature forms of this were also recorded. When populations were high, only a representative sample of the total Aphids was categorised and proportional assessment was made from this.

All relevant predators and parasites were noted, and on most occasions when samples were taken, the degree of parasitism was obtained from an additional collection of Aphids, which was kept alive in the laboratory until an assessment could be made.

Other methods.

Populations of the Pea Aphid on peas can only be sampled by the sweeping method when the crop has been sown either broadcast or in 6-inch drills, as is the usual practice with varieties such as Maple. It is customary, however, to sow peas for culinary purposes in wide drill-widths. Dunn (1951) has described the tip-sampling method which was adopted to meet these conditions and this involves the removal of a given number of growing points from the plants across the diagonals of a plot. When the Aphid infestation is heavy and the colonies are distributed over the plants generally, rather than being localised in their growing points, individual whole-plant samples have to be taken in place of tip samples.

The Crops concerned.

Lucerne.

Population studies were carried out over four consecutive years on the same field of lucerne at Sawbridgeworth, Herts. This large field was subdivided culturally into leys of about eight acres. These leys differed from one another in age and were cut three times a season in order of seniority. The density of each ley varied with its age and generally decreased after the second year of establishment. This, together with the gradation in plant growth and development which the rotational cutting produced, led to different micro-environmental conditions and to inevitable variations in Aphid population levels between leys.

Hop trefoil.

The hop trefoil on which population studies were made was all grown on the same farm at Hatfield Heath, Essex, a different field being used each year.

Hop trefoil is normally undersown in a cereal crop one year, allowed to flower the following spring, cut for seed later and then ploughed in. At Hatfield Heath, therefore, the young hop trefoil, growing through the stubble in its first year, acquired an autumn population of Pea Aphids, and eggs were laid. In the following spring the eggs hatched and large numbers of Aphids were built up.

Sainfoin.

The field of sainfoin which provided population data was located at Great Chesterford, Cambridgeshire. It had been undersown in wheat in 1948, and in the autumn of that year had built up sufficiently high numbers of Pea Aphids to ensure a sizeable population in the succeeding spring.

The crop was cut twice in 1949 and prior to both cuttings, seed pods, which are readily knocked off sainfoin, appeared in the sweeping samples in considerable numbers. The pods, being hard and spiny, crushed many Aphids and made counting difficult. In view of this and because of the similarity of the population data to those from hop trefoil, sampling on sainfoin was not continued after 1949.

Peas.

Most data of a consecutive nature on the populations of Aphids on pea crops were obtained from the Harlow district of Essex. This area represents the nearest pea-growing centre to the Sawbridgeworth lucerne and the hop trefoil at Hatfield Heath. Pea crops here, however, considering their proximity to sources of Pea Aphids, proved of less value in supplying data on population changes than might have been expected. The reason was due essentially to the shortness of the growing season of pea crops destined for picking green. Such crops of peas are often sown early and reach a stage fit for picking shortly after the first migrant Pea Aphids arrive. The Aphids are thus given little time in which to establish sizeable populations before the crop is picked. The situation is additionally complicated by the increasing practice, as a control measure against the Pea Moth (*Cydia nigricana* (Steph.)) of spraying with DDT any crop flowering during June and July. This control measure also checks or prevents colonisation by the Pea Aphid.

Factors that influence the Populations of Aphids.

Several factors cause fluctuations in the population levels of Aphids. The activities of parasites and predators among colonies of Aphids are well known. The production and subsequent emigration of alatae, too, is a factor that can obviously bring about reductions in the numbers of Aphids present in a given population. The condition of the plant, a factor that determines the quality of the food and hence its acceptability and value to the Aphid, alters with age. Freshly growing plants favour rapid multiplication and development of Aphids, whereas mature and dying plants play a negative rôle in this direction. Temperature and rain indirectly affect the numbers of Aphids by influencing other environmental factors; they also directly affect the Aphids.

In the case of temperature, Broadbent (1953) quoted *Myzus persicae* (Sulz.), as undergoing optimum development at 26°C.; below this figure its rate of development declines to a threshold of 4·3°C., whilst temperatures above 28°C. are detrimental. He also made reference to work which showed that the excessive temperatures accompanying hot, dry weather brought about reductions in populations of Aphids. In the case of rain several references are given by Broadbent showing that heavy rain, especially when associated with wind, dislodges Aphids and reduces the population.

Populations in 1948.

Lucerne.

Two lucerne leys of different ages were sampled during 1948. The older ley was sown in 1944 and the younger ley in 1946. The 1944 ley was cut at least three weeks before the 1946 ley on each occasion throughout the season. Sampling extended from 26th April until 11th November when the 1944 ley was ploughed.

The total number and composition of the Aphids taken in 25 standard sweeps at each sampling time are shown in figs. 1 and 2, representing the 1944 and the 1946 ley, respectively. The four Aphid categories, into which each sample was divided, are shown against a background of total numbers. The first occasions on which sampling was carried out over stubble after the crop was cut, are indicated by arrows marked S1, S2 and S3, whilst a heavy downpour of rain, during which anything in the order of half an inch or more was recorded in under 24 hours, is marked R and numbered appropriately.

Fig. 1 shows that the population of Aphids on the 1944 ley was already more than 1,000 per 25 sweeps when sampling began. The potential spring peak was checked when the cutting of the crop on 18th May abruptly brought down the population. On that date immature winged forms predominated and made up 44 per cent. of the total, which meant, through the migration of alatae, a possible exodus from the crop of nearly half the population. This contributed greatly, together with heavy rain, R1, in bringing about the further large depression in the numbers recorded on 3rd June.

Rapid expansion of the population was taking place by 9th June but the rise was further curbed by heavy rain, R2 and R3, combined with larvae and adults of the Seven Spot Ladybird, *Coccinella septempunctata* L. The numbers of both the larvae and the adults of this ladybird, taken per 25 sweeps, are shown in the upper graph in fig. 1 and it will be seen that the ratio of these predators to Pea Aphids was approximately 1:17 and 1:12 on 16th and 30th June, respectively. A considerable degree of control must have been exercised by such ladybird numbers. The ladybird larvae had all pupated by 7th July and most of the adults of the next generation dispersed out of the crop soon after they had emerged. This insect was from thenceforth of much reduced importance in affecting the numbers of the Pea Aphid.

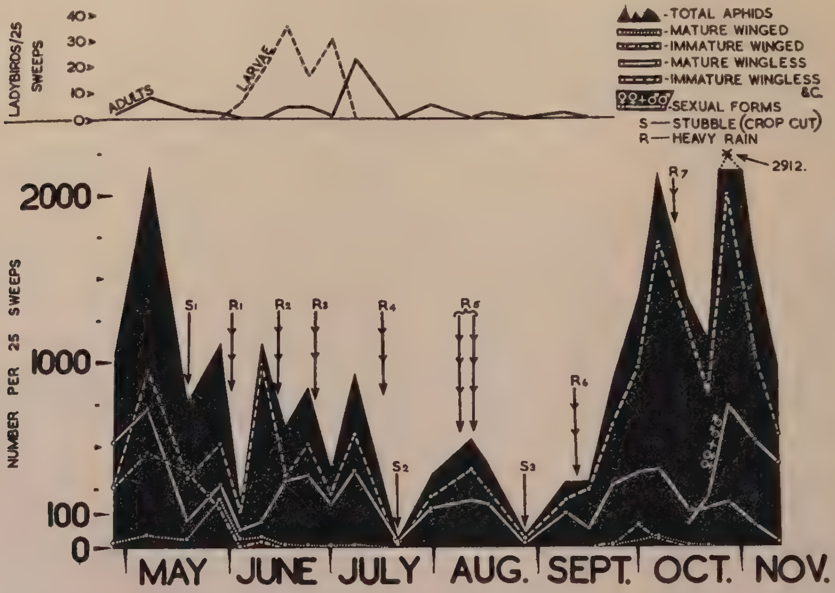


Fig. 1.—Populations of the Pea Aphid on the "1944" lucerne ley at Sawbridgeworth, Herts., 1948.

Rain, R4, and a second cutting of the crop brought the population of Aphids down to a low level by 20th July. Between this date and the third cutting at the end of August, increase of population was restrained by a period of very hot, sunny weather, followed immediately by rain, R5.

The late summer and autumn Aphid population was restricted by rain, R6 and R7, from making full use of the improved conditions of crop growth. A peak in numbers of nearly 3,000 was recorded, however, on 27th October. The populations fell from this date, due firstly to lower temperatures which decreased the rate of reproduction and development, and secondly to the growth of the sexual and terminating Aphid-generation. A ground frost also helped the decline by damaging the lucerne foliage and thus reducing the amount of food available.

On 26th April the 1946 ley supported more than twice the number of Aphids than did the 1944 ley and fig. 2 shows that, unlike the older lucerne, the May peak was not interrupted by cutting. This peak was brought down very rapidly at the beginning of June by the migration of alatae, by rain R1, and by Syrphid larvae. The potential alate population, as measured by the immature forms on 18th May, amounted to 59 per cent. of the total population, whilst the Syrphid larvae were present in numbers between 18th May and 3rd June and as many as 158 were taken in 25 sweeps on 28th May. The lucerne was tending to become fibrous in early June and could have constituted a fourth Aphid-limiting factor at this time, though possibly only in a minor way. This factor, however, was becoming increasingly effective and, combined with rain, R2 and R3, undoubtedly kept the Aphids in low numbers throughout June.

It is interesting to note the difference between the two lucerne leys over the mid-May to end-of-June period. In contrast to the 1946 ley no Syrphid larvae were recorded on the 1944 ley during May. On the other hand, during June, ladybird larvae were present in numbers on the 1944 ley but only one larva was recorded in samples taken from the 1946 ley.

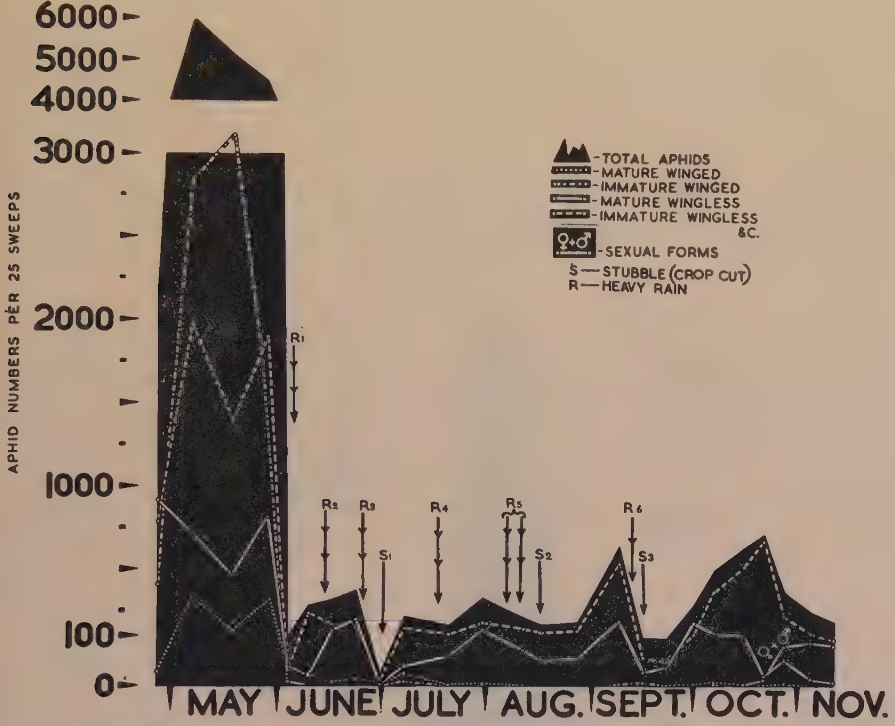


Fig. 2.—Populations of the Pea Aphid on the "1946" lucerne ley at Sawbridgeworth, Herts., 1948.

The absence of Syrphid larvae on the older crop is thought to be due to the cutting and removal of the crop on 14th and 15th May, leading to a simultaneous removal of any Syrphid eggs and young larvae adhering to the foliage. The occasion of this cutting, judging from the 1946 ley, must have immediately followed the peak Syrphid deposition of eggs.

The discrepancy between the two leys in the case of ladybird larvae seems to have no obvious explanation. The respective numbers of Aphids on the two leys when ladybird adults were ovipositing, were not sufficiently dissimilar to induce a marked egg-laying preference in the direction of the 1944 ley. The crop conditions differed; the 1944 ley was making fresh growth whereas the 1946 ley was maturing and becoming fibrous, but discrimination by ladybirds on this basis seems unlikely. After the ladybirds had oviposited, however, the different crop conditions had an effect on the respective populations of the Aphid during June. The numbers of Aphids on the two leys were almost equal on 3rd June, but the fresh plant growth of the 1944 ley promoted greater multiplication than did the fibrous 1946 ley, and led to a faster and bigger recovery in population strength.

Aphid re-establishment on the 1946 ley, following the late June cut, was affected by rain, R4, in mid-July, very high temperatures at the end of this month, then further rain, R5, and another crop cut. More moderate temperatures and drier weather conditions in late August brought an increase in numbers but rain, R6, and a third cut in mid-September brought these down again. This last cut came three weeks later than did the corresponding cut on the 1944 ley and the season by this time was too advanced to allow for a comparable expansion of the numbers of Aphids.

The same factors which reduced the population on the 1944 ley at the end of October, namely, low temperatures, the appearance of sexual forms and frost damage, operated against the Aphids on the 1946 lucerne and brought their numbers down from a peak late in October.

Hop trefoil.

The graph of weekly sweeping records obtained from hop trefoil in 1948 is shown in fig. 3. Sampling began on 16th April and continued until the crop was cut and harvested for seed on 20th July.

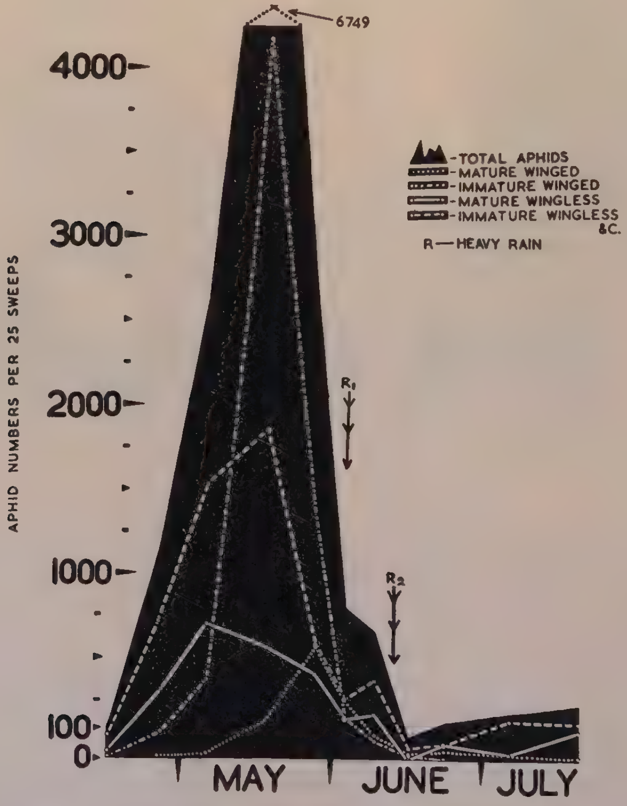


Fig. 3.—Populations of the Pea Aphid on hop trefoil at Hatfield Heath, Essex, 1948.

It will be seen that the number of Aphids rose acutely from the first sampling date to a peak on 18th May and that it fell again even more sharply to the beginning of June. From then it fell further, but after 16th June a slight rise was recorded.

The large number of immature winged forms found on 18th May, amounting to 62 per cent. of the total Aphids, makes it obvious that the migration of alatae probably played a major rôle in the population fall. Rain, R1, helped additionally in this direction and increasing crop maturity might just have begun its influence in early June. On 28th May, when the highest proportion of predators was found, the ladybird larval population averaged one larva per 40 Aphids. Syrphid larvae were also taken on this date but their numbers were much smaller. Predators, therefore, must also have accelerated the decline in the numbers of Aphids.

The surprising feature of the population between mid-June and 20th July was that it managed to increase, though in an extremely gradual manner on a crop which was becoming progressively more mature and desiccated. No sudden growth in the population could, of course, be achieved under such host-plant conditions. It might be that the periodic rain which fell over the time concerned, though insufficient to reduce the number of Aphids, revived the nutritive value of the crop sufficiently for the Aphids to maintain and slightly to increase their numbers.

Peas.

In 1948, two crops of peas (in the Harlow area) for the green-picking trade were sampled periodically by the tip-sampling method. One crop had been sown at the beginning of April for early picking and the other in early July for very late picking. The former crop was the variety Onward and the latter crop the Kelvedon Wonder variety.

Both series of samples are included in fig. 4 and the graphs represent only the total Aphids taken in 100 tips on each occasion.

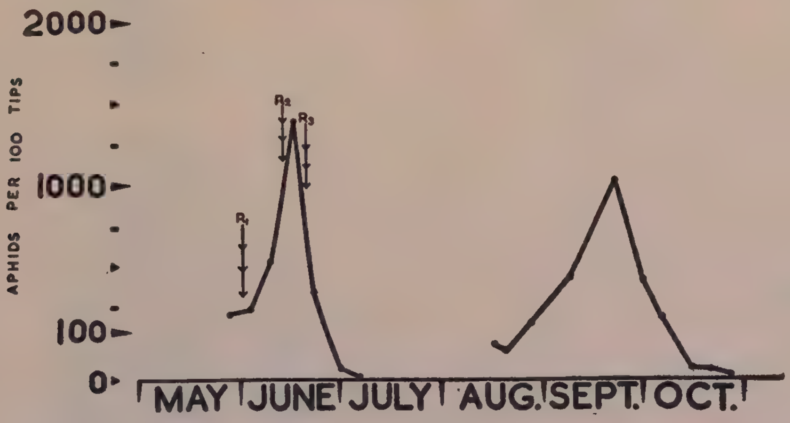


Fig. 4.—Populations of the Pea Aphid on early- and late-sown peas at Harlow, Essex, 1948.

The two graphs show a similar type of curve; a steady rise in population followed by a corresponding decline. The first graph shows that rain, R1, caused an early setback in numbers between the first two counts. Rain, R2, also occurred on 14th June and probably prevented the recording two days later of much higher numbers. To what extent the Aphids dispersed down from the tips of the plants, *i.e.*, out of the sampling area, as a result of disturbance factors like rain, is not known, but colonisation of the lower regions of the plants was never very apparent. The decline in numbers recorded after 16th June is therefore thought to have been the true state of the population. Rain, R3, and the activities of adult and larval ladybirds and Syrphid larvae were the agencies responsible for the depression. No figures were recorded for the numbers of ladybirds because both adults and larvae are too active to be taken by the tip-sampling method; many were seen, however, whilst sampling was in progress. The Syrphid larvae occurred in the ratio of one larva to every 50 Aphids on 16th June. A small amount of fungal disease was also noted at this time.

The second graph is a little flatter than the first, but shows a similar check between the first and second sampling dates. Once more the operating factor was probably rain which occurred in local thunderstorms over the first half of August. The factors bringing about the decline, seen after 22nd September, were Syrphid larvae, fungi and rain, combined with a progressive drop in temperature as the season advanced. On 30th September the ratio of Syrphid larvae to Aphids was 1:70 and on 6th October the ratio was 1:40.

Populations in 1949.

Lucerne.

The 1946 ley used in the population studies of 1948 and an adjacent lucerne ley which was sown in 1947 were sampled in 1949. The two leys were cut within a few days of one another on each occasion and their respective populations behaved very similarly, both in numbers and composition, throughout the season. The graph for the 1946 ley is given in fig. 5 and shows an almost complete reversal of the picture obtained of the total numbers of Aphids for the same ley in the previous year.

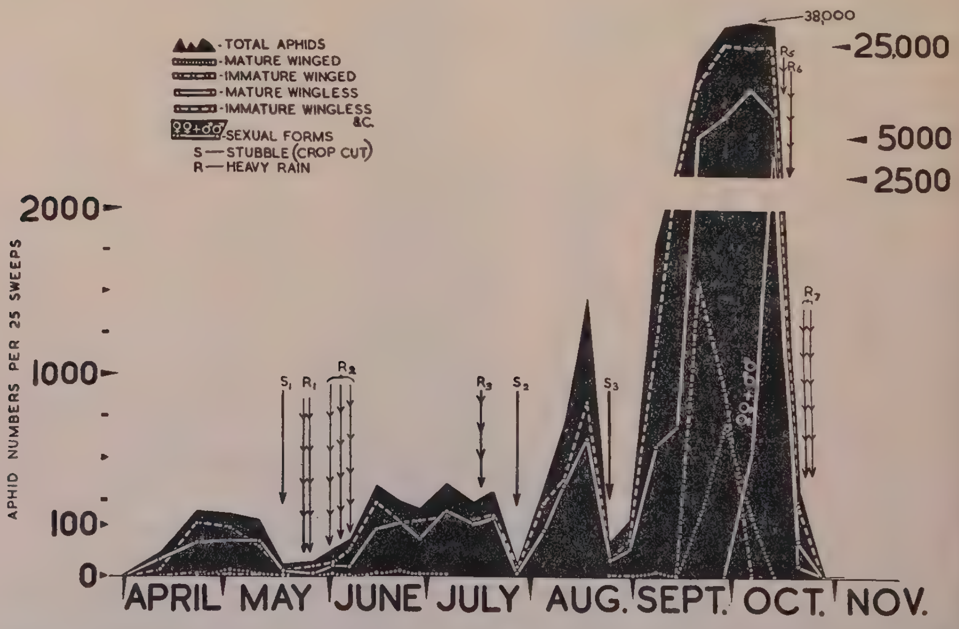


Fig. 5.—Populations of the Pea Aphid on the "1946" lucerne ley at Sawbridgeworth, Herts., 1949.

Sweeping began on 31st March when, after a mild winter, only one Aphid was found in twice the customary number of sweeps. A slow rise in the population followed which gave way to a slow decline accelerated by crop cutting just before 18th May. From the 12th April to the end of that month, a period of very hot weather, unique for the time of year, was experienced, during which screen temperatures sometimes exceeded 80°F. Under such conditions, crop level and foliar-surface temperatures would have been sufficient to retard Aphid reproduction and slow down the population rise. In addition, the fundatrices and subsequent generations in spring were subjected to an unusually early and intense parasite attack. It was estimated that approximately 50 per cent. of the fundatrices were killed by parasites. This would result in a setback to potential springtime numbers which must have expressed itself over more than one generation, even if no further parasitism had occurred. Meanwhile the incidence of parasitism increased and was a main factor in curbing the Aphids until mid-June, when hyperparasites appeared.

In the spring population of Aphids, the numbers of both immature and adult winged forms were few and they represented lower percentages of the population than in 1948. They were, therefore, relatively unimportant in causing a depletion in the numbers of Aphids.

Following the fall in population seen on 18th May, due to cutting of the crop, the population recovery was very slow. The agencies that restricted increase were parasites and rain (R1 and R2), followed later by a period of cloudless, hot, sunny weather. The rain, R2, marked on the graph as extending over the first few days in June, was not continuous but in the form of spasmodic and very heavy thundershowers.

Between the depression after the second cut of the crop, S2, and the third cut on 24th August, a fairly sharp peak in the numbers of Aphids was produced. Almost coincident with the third cut of the crop, excessive heat once more restricted maximum reproduction but the cooler, sunny days of September soon provided ideal temperatures for population expansion. In addition to optimum conditions of temperature, other factors proved highly favourable to an increase of Aphids and helped to produce the kind of population numbers seen in fig. 5. The primary parasites, for example, had been quickly subjugated by hyperparasites in the first half of July and were no longer a factor imposing limitations on the numbers of Aphids.

A series of records showed that up to the last week of June the incidence of primary parasitism among the Aphids stood at over 50 per cent. This figure had fallen by 14th July to nine per cent. and from 27th July onwards no more than two per cent. primary parasitism was recorded. On the other hand, hyperparasites were not observed until the end of June and by the end of July almost all sessile Aphids were found to contain hyperparasites. Predators also, although never very common in the lucerne with its low spring and summer populations of Aphids, were almost entirely absent during September. Furthermore, the lucerne itself was growing rapidly and providing an expanding food supply. Lastly, no heavy rain of an Aphid-destroying character fell during September or early October.

Thus, in nearly optimum environmental conditions for development, the population multiplied prodigiously and reached dimensions in which the Aphids became limited by available food supply. The numbers were so great at the beginning of October that the ground was nearly covered by cast skins and the lucerne was suffering much damage. The lucerne plants, in ever widening patches, began to die and it was estimated that between 50 and 60 per cent. of the total number of shoots in the ley as a whole were killed. In mid-October the number of Aphids began to decline rapidly as a result of overpopulation. This trend was accelerated by increasing numbers of Syrphid larvae and lower daily temperatures. From 18th October, rain moved the decline into landslide proportions. Heavy ground frost at the end of the month provided a final check by killing off the summer foliage of the lucerne. The majority of Aphids in mid-October were immature or mature sexual forms and oviposition had not fully begun when the population was virtually eliminated; as a result, the over-wintering egg population was very low.

The numbers of Aphids at the time of highest infestation were so great that they had to be assessed by weighing. Most of the foreign matter was first removed from the sample and a small portion of Aphids, between about 5 and 10 per cent. of the total, was weighed and categorised. The result was then used for calculating and proportioning out the numbers in the whole sample, the weight of which had also been found.

The 1947 lucerne showed the build-up of an even higher autumn peak than did the 1946 ley, a maximum count of nearly 44,000 Aphids per 25 sweeps being recorded. The density-limiting factor also came into operation in this case but at a higher population level. The lucerne had been cut a week earlier than the 1946 ley and had made taller and more dense growth. A greater volume of food was therefore available and a higher maximum population of Aphids could be supported.

Hop trefoil.

The graph, fig. 6, shows that sampling on hop trefoil in 1949 extended from 22nd April to 6th July. The curve obtained is not dissimilar to that of the previous year (fig. 3) and shows that the population reached a peak in mid-May,

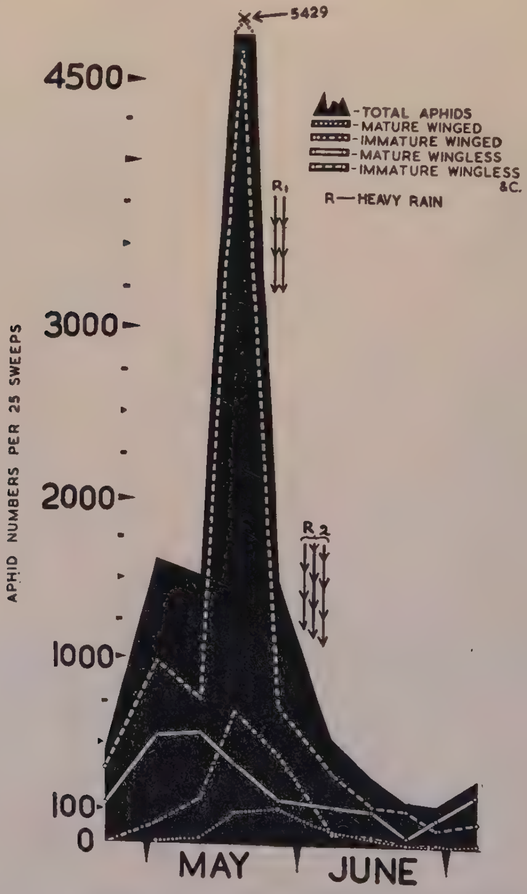


Fig. 6.—Populations of the Pea Aphid on hop trefoil at Hatfield Heath, Essex, 1949.

which fell abruptly by the end of that month. The decline then slowed down and afterwards showed a slight rise in early July.

Parasites, combined with high temperatures in the latter half of April, also affected the Aphids on hop trefoil as they did in the case of those on lucerne. Between 80 and 90 per cent. parasitism was recorded in May and the dip in the upward trend of the curve in fig. 6 between 2nd and 11th May reflects the influence of this and shows that the whole development of the population of the Aphids was effectively put back more than a week. Without this retardation, the population might, in the more favourable weather which followed April, have reached a peak considerably in excess of the one achieved on 18th May.

The major decline in the population was brought about by rain, R1, which fell on the night of 28th May, and by parasites. The migration of winged forms could not have caused a very pronounced fall in the number of Aphids, since the immature winged forms, at the time of their maximum numbers, totalled only 12 per cent. of the population. This contrasted markedly with the 62 per cent. of potential alatae found on trefoil in 1948. The decrease in the numbers of Aphids continued throughout June, parasites and rain being the main factors concerned. The crop-maturation factor became increasingly more prominent as July approached but, in spite of this, the Aphids showed a slight numerical increase just before the cutting of the crop. This confirms the previous year's findings and leads to the conclusion that, in spite of its brown and dry appearance, hop trefoil remains sufficiently nutritive to support fair numbers of Pea Aphids until the crop is cut for seed.

Sainfoin.

The numbers of Aphids swept on sainfoin in 1949 are shown in the graph, fig. 7.

Considering the large population present at the end of March, the rate of increase in numbers during April and early May was slow, being reduced, as in the case of hop trefoil, by parasitism and high temperature. The incidence

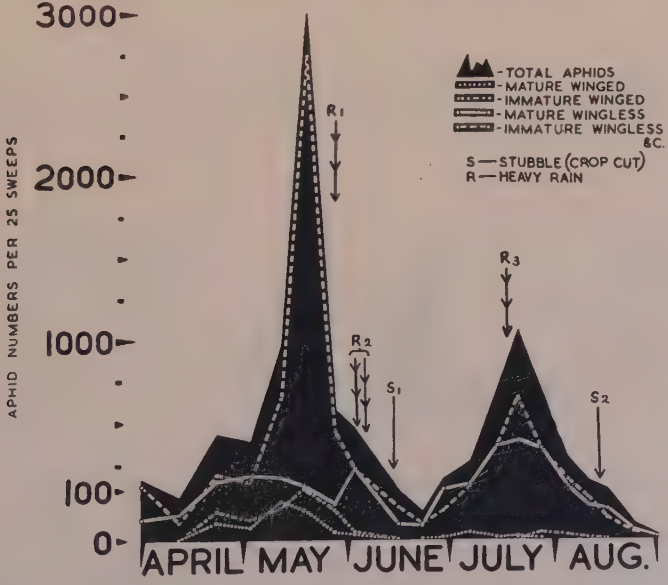


Fig. 7.—Populations of the Pea Aphid on sainfoin at Great Chesterford, Cambs., 1949.

of parasitism was 52 per cent. as early as 31st March, and the two depressions in the population curve before 11th May are thought to reflect a generation effect on the part of the parasites.

The May peak rose and fell in a manner similar to the hop trefoil population and the same greatly accelerated rate of Aphid reproduction, indicating a brief easement in the natural controlling factors, also occurred.

The low production of winged forms on sainfoin confirmed the findings on the other two host crops, and migration could only have been a subsidiary depletion factor in bringing about the decrease from 18th May. Parasites, rain and cutting of the crop were the main agencies. Fungal disease also influenced the population decline to some extent. Later the incidence of primary parasitism fell in the face of hyperparasite attacks and from mid-June became a decreasingly important Aphid-controlling factor.

On 15th June, primary parasitism among the Aphids amounted to 75 per cent., by mid-July this figure was only nine per cent. and in August no Aphids were found to be parasitised. Hyperparasites, however, had grown rapidly from low numbers in June to total incidence among sessile Aphids by August.

A small peak in the numbers of Aphids was slowly attained in the latter half of July despite hot sunny weather and some rain. The host crop, however, was growing up in fresh condition from a cut in June and the parasite influence had waned. These two latter conditions should have favoured a high rate of Aphid multiplication but the relatively large proportion of mature forms seen in fig. 7 indicates that, although total numbers rose, the reproductive rate did not surge upwards as it did in May. The control exercised on the population by high environmental temperatures was, therefore, considerable.

Towards the end of July the sainfoin began to mature very quickly and by the time it was cut for seed in mid-August was very desiccated. Hot weather and rain under these host-crop conditions brought the population down, whilst cutting reduced it still further. The high stubble which remained did not regrow and when the sainfoin was ploughed in in mid-September the numbers of Aphids were down to 5 per 25 sweeps.

Peas.

A field of Maple peas at Harlow was sampled in 1949 over a period extending into three months. This crop had been sown in six-inch drills and was sampled by sweeping. The graph of the numbers of Aphids obtained by this method is shown in fig. 8.

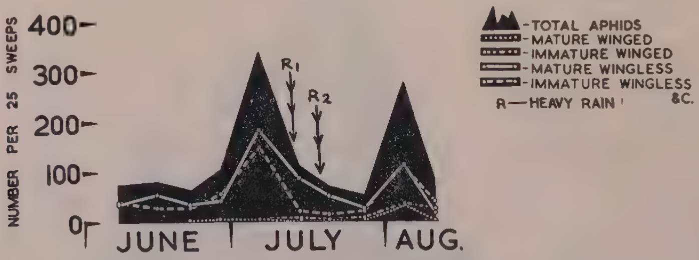


Fig. 8.—Populations of the Pea Aphid on Maple peas at Harlow, Essex, 1949.

The June population on the field can be seen from the graph to have remained fairly static until the end of the month when a slight rise in numbers began; high temperatures and parasites had restrained an increase up to this time. The incidence of parasitism on 22nd June was estimated at 63 per cent. The appearance of alatae in the sample taken on 22nd June preceded the finding of immature winged Aphids on peas by three weeks. This showed that there was another influx of migrants into the crop coincident with, and presumably fostering the population rise.

Rain, parasites and Syrphid larvae brought down the number of Aphids in July. In the case of parasites, 34 per cent. parasitism was recorded on 14th July but the incidence fell to eight per cent. by 10th August. In the case of Syrphids, their larvae occurred in the ratio of one to approximately 34 aphids on 27th July but by 10th August only pupae were recorded. As the parasite and predator factors lessened in intensity an increase in the population took place. Higher temperatures prevented this increase from being rapid, and later, when the crop began to mature, the hot weather, combined with the less favourable plant growth, produced a fall in the numbers of Aphids. The decrease was augmented by the emigration of winged Aphids which can be seen in fig. 8 to have been produced in ever growing numbers.

Two other fields of peas, one at Hatfield Heath and the other at Manea, Cambridgeshire, provided consecutive sampling data in 1949.

The Hatfield Heath peas were the variety Onward and a series of tip-samples was obtained from them between 2nd May and 6th July. The population here was extremely light throughout the sampling period, and at maximum amounted to only 117 Aphids per 50 tips. As a result, other than a slow initial build-up to unspectacular numbers, population trends were inconclusive. Winged migrants were found on and between 11th to 27th May. This represented an influx into the crop rather than a production on it, for immature winged forms did not appear until 22nd June. This finding is consistent with the production of winged forms on the winter host-crops.

The population on the Harrison's Glory variety of peas at Manea was also assessed by tip sampling. Small numbers of Aphids were present at the end of May and these produced a minor peak on 7th June. A decline in the population soon followed but it was superseded at the end of June by a second and main peak in the numbers of Aphids. The population decreased sharply in July. The trough after the first peak was probably the result of parasite activity for though no assessment of parasitism was made sessile Aphids were seen to be numerous. The final decline in early July was chiefly due to Syrphids. Larvae of the latter occurred in the ratio of 1 per 12 Aphids on 20th July. Fungal disease and crop maturation also played small rôles in the final decline of the population of the Aphid.

Populations in 1950.

Lucerne.

The 1946 ley was sampled during 1950 for the third consecutive year. An adjacent lucerne ley which was sown in 1948 provided a companion series of population samples.

Fig. 9 shows the changes in the population on the 1946 ley; no graph for the 1948 ley is included as the numbers of Aphids on the two leys were comparable up to the end of July.

Owing to the small number of overwintering eggs, a reflection on the virtual decimation of the oviparous female populations at the end of October 1949, the numbers of Aphids in the spring of 1950 were extremely low. Inclement weather during April and May considerably inhibited population expansion. After cutting on 23rd May, the lucerne, stimulated by rain, grew very rapidly in the period of fine weather from the end of May to mid-June. In the near optimum temperatures for development of between 70° and 75°F. which the fine weather provided, the population multiplied quickly on the lush plant growth and produced a peak in numbers at the end of June.

The population fell abruptly in face of some very heavy thunderstorms in the second week of July, which at the same time battered and laid the crop. The emigration of winged forms, as in the previous year, played only a subsidiary part in depleting the population. Thus it will be seen in fig. 9 that, at the time of the June peak in numbers, immature winged forms made up only 10 per cent. of the total. On the adjacent 1948 ley the proportion was even lower and constituted 8 per cent. of the total Aphids at their June peak. Parasitism was probably of similar importance to the migration factor in reducing numbers and, over the period of their decline, the incidence was between 10 and 12 per cent. Predators were of even less importance and, of these, ladybirds which occurred in the ratio of about one to every 600 Aphids on 26th June, were the most commonly found.

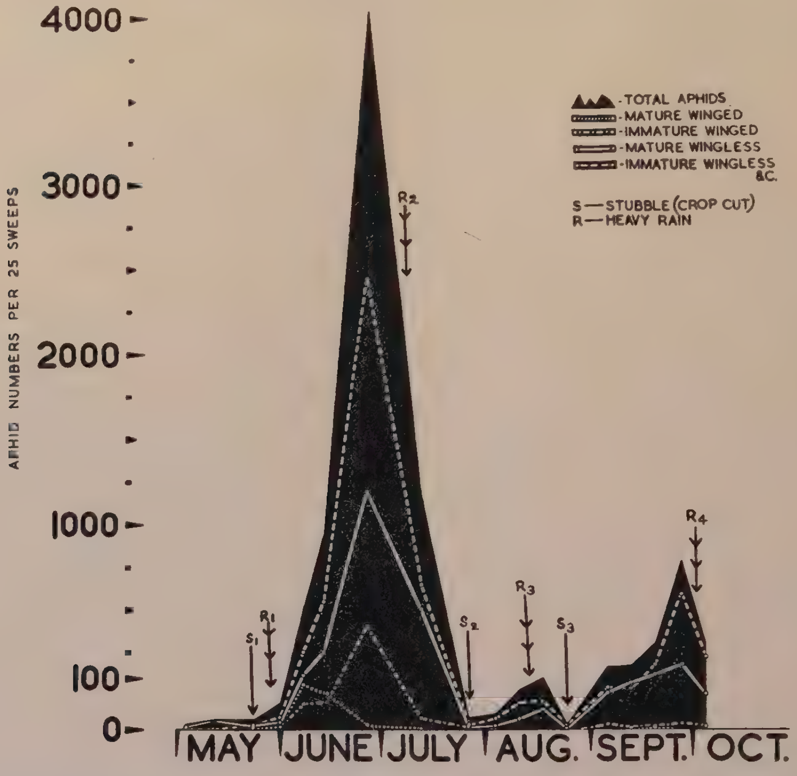


Fig. 9.—Populations of the Pea Aphid on the "1946" lucerne ley at Sawbridgeworth, Herts., 1950.

The second cutting of the crop on 26th July brought the population down still further. Aphid recovery from this cutting was slow and only very small numbers had been reached when the crop was cut for the third time on 24th August and the population was once more reduced. Factors preventing a more rapid increase during August, on a crop which was growing rapidly, were Syrphid larvae, some high temperatures and rain, R3. On 3rd August one Syrphid larva was found to every three Aphids, but as the larvae pupated this ratio later widened in favour of the Aphids.

A small peak in the numbers of Aphids was recorded in late September following a slow and unsteady rise in population subsequent to the third cutting of the crop. Relatively cold weather with frequent rain limited more obvious multiplication, whilst, at the same time, favoured by the weather, fungi spread among the Aphids to an extent not previously found in a crop of lucerne. It was estimated on 12th September that nearly 30 per cent. of the population were infected. Before the crop was ploughed in early in October, rain, R4, reduced the population, the rate of expansion of which was also being inhibited by lower temperatures.

The 1948 ley was not cut for the third time until 19th September and the Aphids were able to reach a much higher and earlier September peak in numbers, than was the case on the 1946 ley. After the cut, however, the much reduced population which resulted never recovered and persisted through into November in extremely low numbers. The sexual generation made its appearance here from mid-October.

Hop trefoil.

The population of the Aphid on hop trefoil at Hatfield Heath in 1950 has been dealt with by Dunn (1951). He showed that a spring peak in numbers was established in June but did not reach the heights of the two previous years. As in the case of lucerne in 1950 the production of winged forms on trefoil was also low. Dunn also described the development in October and November of the population on the trefoil field used for studies in 1951.

Peas.

The 1950 populations of the Aphid on certain pea fields in Essex have likewise been described by Dunn. On a field of Maple peas the June population reached such high numbers that the grower resorted to chemical measures as a means of control. A reduced incidence of fungal disease and predators, in a field of late-sown Kelvedon Wonder peas, enabled infestation by the Aphid to reach higher than average numbers. Rain, lower temperatures and renewed Syrphid activities, however, soon brought these numbers down.

Populations in 1951.

Lucerne.

A lucerne ley at Sawbridgeworth in its second year of establishment was sampled at intervals between 26th April and 6th October 1951. The population graph obtained is shown in fig. 10.

It will be seen that from the beginning of sampling until the cutting of the crop brought the populations down on 5th June, the Aphids did little more than double their numbers over a period of six weeks. The rise even so was far from direct and was achieved in stages. The weather over the period was most directly responsible for the slow Aphid development. The few fine days which followed the first sampling were succeeded, until the last week in May, by a period of relatively cold unsettled weather with frequent heavy rain. In such conditions effective expansion of the numbers of Aphids was impossible, especially when, simultaneously, the incidence of parasitism was between 20 and 25 per cent. The parasite attack, however, although fairly consistent in its degree of intensity up to about mid-July was insufficient to check the rising numbers of Aphids during June. Greatly improved weather conditions, combined with host-crop regrowth, brought about the increase to peak numbers which were reached on 9th July. Rain, and cutting of the crop about the middle of July again brought down the number of Aphids to a low level. Very hot weather and rain, R3, produced a further reduction in numbers by 14th August.

The emigration of alatae was of little importance in depleting the population and the proportion of winged forms produced on lucerne in 1951 was the lowest since the population studies began. It is shown in fig. 10 that less than one per cent. of the total Aphids in the peak of 9th July were immature winged forms. A population sample obtained in the last week of June might have shown a higher proportion of potential winged forms than did the record on 9th July, but not, it is thought, to any substantial degree.

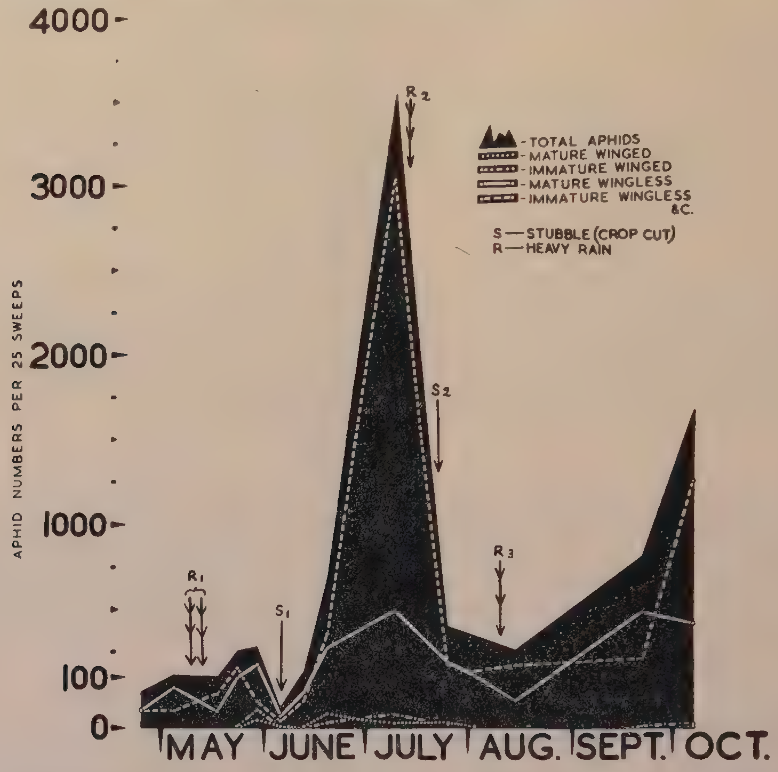


Fig. 10.—Populations of the Pea Aphid on lucerne at Sawbridgeworth, Herts., 1951.

A gap in sampling records occurred between 14th August and 21st September and an increase in the population over this period is shown in the graph. The weather at the end of September and early October was clear and sunny and a further rise in numbers was recorded on 6th October. The usual autumn development of small numbers of winged forms took place from mid-September but sampling was not continued long enough to show the formation of the sexual generation.

Hop trefoil.

The same field of hop trefoil at Hatfield Heath, on which egg counts were made over the winter of 1950–51, was swept periodically between 24th April and 9th July 1951. The populations so found are shown in fig. 11.

The cold, unsettled, stormy weather during May which restricted the increase in numbers of Aphids on the lucerne at Sawbridgeworth, produced a similar effect on the Aphid populations on hop trefoil. Parasitism in early May was also a factor in limiting multiplication. A low peak in numbers of Aphids was recorded on 19th June, following a general improvement in the weather. When the population was assessed again on 9th July, the crop had matured considerably and a slight drop in numbers was seen to have occurred. Ladybird larvae had begun to appear by this date and were probably exercising some control. The production of winged forms was extremely low and migration of alatae as well as the parasite factor, which had declined from mid-May, were but minor agencies depleting the numbers of Aphids from mid-June.

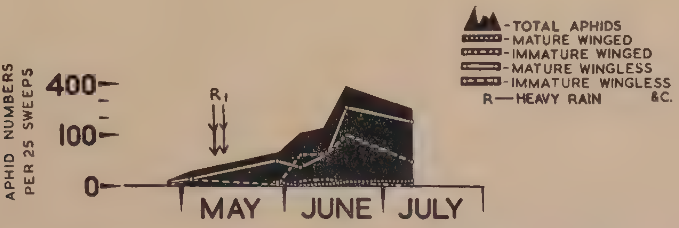


Fig. 11.—Populations of the Pea Aphid on hop trefoil at Hatfield Heath, Essex, 1951.

Peas.

The numbers of Aphids were exceptionally low in all fields of peas visited in Essex during 1951. This was undoubtedly because very few winged forms had been produced in spring on the overwintering host-crops. It was, therefore, not possible to obtain any data on population development and fluctuations on peas.

Discussion.

The population data on the Pea Aphid show considerable annual diversity. Each year it is apparent that one or more different factors operated against, or in favour of, expansion in the number of Aphids. This Aphid has a very high potential rate of population increase but field conditions are only occasionally favourable enough to allow this to be achieved, as in the autumn of 1949.

A critical analysis of the agencies underlying population restrictions is not possible in the absence of exact knowledge on the influence exerted by one factor working by itself, let alone in variable combination with other factors. Some factors bring about obvious and clear-cut reductions in the number of Aphids, for example, heavy rain and crop cutting, but even here, following the altered relationship between the Aphid and its environment, other effects are produced. The cutting of the crop mechanically destroys some Aphids and many more disappear from the field in the crop during its removal. Anything else adhering to the foliage is also removed; this applies to sessile, parasitised Aphids and to ladybird, hover fly and other predator eggs. Following cutting, therefore, the Aphids which escape destruction may not only benefit from the greatly improved food conditions provided by the freshly growing aftermath but may also enjoy an environment relatively free from insect enemies. This especially would be the case if cutting and removal of the crop followed upon heavy and widespread oviposition by one or more species of predator. The suspected reason for the absence of Syrphid larvae in 1948 on the 1944 lucerne ley is an illustration of this point. Alternatively, if most of the predators are in an active stage and/or most of the parasites in the adult stage by the time that the crop is removed from the field, conditions might operate against the Aphids, by permitting the survival of a disproportionately large number of natural enemies. Rain at the time of cutting of the crop may help to stimulate the growth of the aftermath and indirectly enable a more rapid multiplication of Aphids. On the other hand, the reduction in foliage volume which cutting entails leads to greatly lessened shelter and the removal to a large extent of the protective "cushioning" layer of air at crop level; the Aphids which remain are, in consequence, rendered more vulnerable to rainstorms.

The retardation effect exercised by high temperature on populations of Aphids is also subject to reservations. The data on the Pea Aphid show that in East Anglia hot summer weather checks and reduces populations only when the crop is becoming less palatable. When the crop is young and freshly growing, populations can increase slightly under hot summer conditions. Plant maturation, however, rapidly hastened in such weather, soon reaches the point of decreasing palatability.

The importance of the migration factor in depleting populations of the Pea Aphid on the overwintering host-crop varies each year. On the overwintering hosts the relative variation in percentage production of winged forms has been found to be much greater between different years than between different host-crops. On lucerne there are two definite peaks in the production of alatae, one in spring and another in autumn, with production discontinued during the intervening months of July and August. Thus, in spring and autumn, and especially during the former, the emigration of winged forms plays a part in the seasonal decline of the populations on lucerne but any reductions in the number of Aphids on this crop during summer is independent of the migration factor. The emigration of winged forms can constitute a population-depleting factor during summer in the case of the pea crop. Invariably, however, the period of growth of this crop is too short for the production of alatae to become a marked feature of the population.

The wide annual variation in the percentage production of winged forms of the Pea Aphid in spring must have a considerable influence on the total numbers of migrant Aphids and, therefore, be an important factor in determining the level of Aphid infestation on the pea crop. There would seem to be a need for more fundamental studies on the causes underlying the production of alatae.

Predators and parasites have years of high and years of low abundance. The usual requirement for the presence of these natural enemies within a crop is, of course, the presence of the Aphid, and many instances have been observed where a build-up in the population of Pea Aphids has soon produced a corresponding increase in the number of predators and/or parasites. This means that the Aphids generally have the advantage of initial supremacy, to overcome which the natural enemies require time. During this time the numbers of Aphids may also be, and often are, affected by heavy rain, crop maturation or high temperatures. Thus predators and parasites are invariably complementary controlling agencies, and there have been few occasions throughout the population studies when natural enemies have obviously been prime controlling factors of the Pea Aphid.

Summary.

Data on the populations of the Pea Aphid, *Acyrthosiphon pisum* (Harris), have been accumulated over four years on several leguminous crops in East Anglia. The populations on lucerne have provided the most extensive studies.

Considerable annual variation was shown by the populations, but in spring the development of a peak in the numbers of Aphids occurred on lucerne, hop trefoil and sainfoin. On lucerne, which was periodically cut, the Aphids persisted throughout the growing season and a tendency towards the development of a peak in numbers in the autumn was also recorded.

All the factors which affected the number of Aphids varied considerably in the influence they exerted. The probable reason for the more obvious trends in the populations have been given in fairly broad outline, but how the effect of these factors had been altered or predisposed by less apparent factors has been speculated upon only in certain instances.

The biological agencies in the form of parasites, predators and fungal diseases had periods of especial abundance but appeared to exert a much less marked control of the Pea Aphid than did certain physical agencies.

The vulnerability of the Pea Aphid to heavy rain has been shown and the latter was found to be one of the most consistent factors in reducing populations.

The retardation effect exercised by hot summer weather in East Anglia checked and reduced populations only when the host-crop was becoming less palatable.

There was a wide annual variation in the percentage production of winged Pea Aphid forms in spring, and hence emigration, as a factor depleting the population, was correspondingly variable. On lucerne, hop trefoil and sainfoin the relative variation in percentage production of winged forms was found to be much greater between different years than between the different host-crops. There was also a small development of winged forms in the autumn on lucerne.

Acknowledgements.

The writers are indebted to the Agricultural Research Council for a grant which financed the investigation and to the various farmers from whose fields the data were obtained.

References.

Broadbent, L. (1953). Aphids and virus diseases in potato crops.—Biol. Rev., **28**, pp. 350–380.

Dunn, J. A. (1951). Pea Aphid population studies in 1950.—Rep. nat. Veg. Res. Sta., 1949–50, pp. 21–26.

OVERWINTERING EGG POPULATIONS OF THE PEA APHID IN EAST ANGLIA.

By J. A. Dunn and D. W. Wright
National Vegetable Research Station, Wellesbourne, Warwick.

The majority of the population studies made in East Anglia on the Pea Aphid, *Acyrthosiphon pisum* (Harris), have been carried out on the active stage of this insect. The fate of the inactive stage, that is, of the overwintering eggs, has also been followed, and a series of egg counts was obtained during the winter of 1950–51. These egg counts were made on a field of lucerne, *Medicago sativa*, at Mepal, Cambridgeshire, and on a field of hop trefoil, *Medicago lupulina*, at Hatfield Heath, Essex.

Both fields had an autumn population of Pea Aphids, and an area of 50 × 10 yards where the plant growth was most uniform was selected for sampling within each field.

Samples were taken from each plot at intervals throughout the winter; the method consisted of the removal of all foliage from ten six-inch lengths of row across each diagonal. The distance between each sampling point was about five yards. The foliage was removed by cutting it down at ground level, the tops having first been carefully gathered together in the hand to prevent Aphid material from dropping out. The soil immediately surrounding the cut length was also thoroughly examined for any Aphids which might have been dislodged accidently during the operation. Over-removal of the plants along the diagonals, following repeated samplings, was obviated by traversing lines just off, but parallel to, the diagonals and by slightly varying the first sampling point relative to the distance into the plot.

Lucerne.

The lucerne was about 15 inches high when sampling for eggs of the Pea Aphid began on 2nd November. The Aphids found were subdivided into viviparae, oviparae, males and immature forms. The eggs were categorised according to maturity into green, dark, and black, their position on the plant also being recorded.

Two graphs are shown in fig. 1, one representing the numbers of eggs and the other representing the numbers of Aphids which were found per 20 six-inch row lengths on each occasion. It will be seen with regard to the Aphids that, from a peak in number in excess of 700 on 8th November, the population had dropped to *nil* by January. Fungal disease helped considerably to accelerate this fall. The viviparae, present in small numbers on 2nd November, had completely given way to sexual forms three weeks later. The first Aphids to emerge from eggs the following spring appeared in the sample of 15th February. These fundatrices rose to a peak in numbers in mid-March and fell away again until production of the fundatrigenae began about 20th April and swelled the total numbers. The fungus, present from the previous year, was largely responsible for the drop in the number of fundatrices. Very soon after the appearance of the fundatrigenae the entire population was decimated by this agency.

The egg population on 2nd November was found to be 39 per 20 six-inch lengths of row. More than half of these were green, freshly laid eggs, indicating that oviposition was not long started. No green eggs were found later than December, which, as might be expected, coincided with the disappearance of the oviparae.

The apparent drop in the numbers of eggs seen on 9th January undoubtedly resulted from failure to detect many eggs during examination, the foliage, which was largely dead, being in a very wet, unfavourable condition on that occasion. From 22nd January the numbers of eggs found on the foliage fell away to *nil* by 13th March.

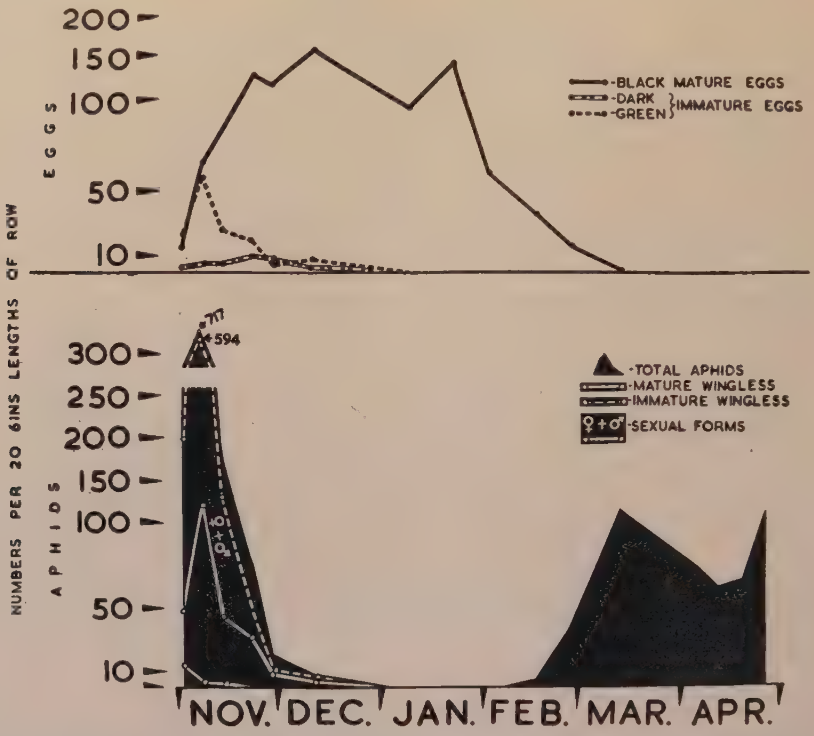


Fig. 1.—Overwinter populations of Aphids and eggs on lucerne at Mepal, Cambs., 1950–51.

Hop trefoil.

Sampling of the egg population on the hop trefoil began on 19th October. Any Aphids and eggs which were found were sub-divided as described for those found on the lucerne, and their numbers are shown in the graphs of fig. 2.

During autumn, the general development of the population on the hop trefoil lagged behind that on the lucerne. It was not until the third sample was taken, on 6th November, that sexual forms were first recorded, and then they made up less than 10 per cent. of the total population. In the case of the lucerne, mature sexual forms were found to constitute 25 per cent. of the total population on 2nd November. No asexual forms were found on the lucerne after 14th November whereas they were last found on the hop trefoil on 30th November.

The findings, in relation to the first occurrence of eggs, also bear out the later state of Aphid development on hop trefoil. The underlying reason is thought to be the maintenance, throughout the winter, of much green foliage on hop trefoil, as opposed to the dying out of the majority of the foliage on lucerne. Thus the development and disappearance of autumn forms of the Pea Aphid, influenced to an unknown extent by host-plant condition, would be hastened in the case of lucerne and be more gradual on hop trefoil.

Oviposition on the hop trefoil began just prior to 6th November and continued until late January or early February, probably six weeks later than was the case on lucerne. Peak numbers of eggs were found in mid-December, at which time there were calculated to be two eggs for every inch of length in the row. From the end of January the number of eggs found on the hop trefoil decreased substantially, even before eclosion began. A similar occurrence was noted on the lucerne. The eggs, it is assumed, were either washed off the leaves by rain or were consumed by predators.

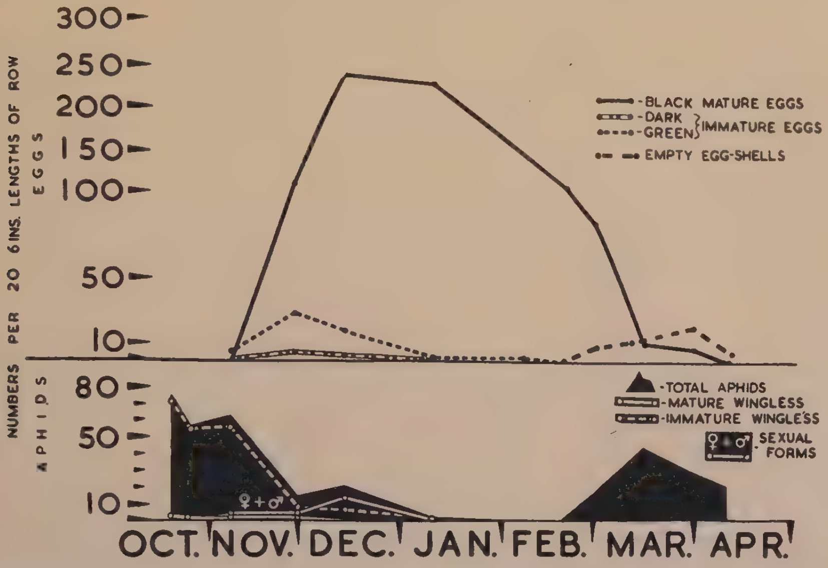


Fig. 2.—Overwinter populations of Aphids and eggs on hop trefoil at Hatfield Heath, Essex, 1950–51.

Exposure to rain and presumably to damage therefrom, is a factor particularly applicable to hop trefoil; of the total eggs found on this crop, 94·4 per cent. were located in open positions on the upper surface of the foliage.

It is of interest to contrast other differences that existed between the two host-crops. There was a considerably larger population of sexual forms in autumn on the lucerne than on the hop trefoil, yet the reverse situation was apparently true of the egg population. Sampling figures obtained of the peak-number of eggs found on both crops are shown in Table I, together with the number of eggs found at the beginning of eclosion and the number of fundatrices at the time of their peak occurrence.

Table I.

Crop	Numbers per 20 six-inch lengths of row		
	Maximum number of eggs found	Total eggs at beginning of eclosion	Maximum number of fundatrices found
Lucerne	163	34	114
Hop trefoil	241	107	48

The fewer eggs but the greater number of oviparous Aphids found on lucerne might infer either reduced fecundity or a shortened adult life in the oviparae

The latter alternative is a possibility in view of the high incidence of fungal disease in this field. It will be seen in Table I, however, that more than twice the number of fundatrices were subsequently found on lucerne compared with hop trefoil. Furthermore, the fundatrix peak of numbers was three times the egg total at the beginning of eclosion on lucerne and in the case of hop trefoil it was only half. There was, in other words, a recovery on to the lucerne of fundatrices emerging from eggs which must have fallen or been knocked off the host-plant. Many more eggs, therefore, than featured in the counts were undoubtedly laid on the lucerne plants, a fact which was also indicated by general observation. As a result, although overwintering mortality was apparent, the extent of its occurrence is unknown. The prediction of outbreaks of the Pea Aphid in summer based upon egg counts made the previous winter would, therefore, not appear to be reliable.

The egg counts made on hop trefoil were probably a fairly accurate assessment of the actual population, and the overwintering mortality, based on the maximum number of fundatrices which resulted, was 83 per cent.

Summary.

Egg populations of the Pea Aphid, *Acyrthosiphon pisum* (Harris), overwintering on lucerne and hop trefoil have been followed. On hop trefoil the overwintering mortality of these eggs was 83 per cent. Although the mortality was apparently less on lucerne, a wide discrepancy existed between the two crops in the ratio between the total numbers of eggs at the beginning of eclosion and the number of Aphids which successfully established themselves the following spring. The peak number of fundatrices on lucerne was three times the egg total at the beginning of eclosion whereas on hop trefoil it was only half. Many more eggs than were recorded were undoubtedly laid on the lucerne plants and the high number of fundatrices subsequently found must have emerged from eggs that had fallen or been knocked off the host-plant.

EGG-PRODUCTION IN THE MUSTARD BEETLE, *PHAEDON COCHLEARIAE* (F.) IN RELATION TO DIETS OF MINERAL-DEFICIENT LEAVES.

E. M.

By M. Delia Allen and Ireson W. Selman

Department of Biological Sciences, Wye College, University of London, Wye, Kent.

Attention has been directed by Painter (1951), and others (*e.g.*, Allen, M. D., unpublished thesis, University of London, 1954) to observations concerning the effect on the insect of nutrients supplied to the food-plant. Many of the records are field observations made under ill-defined conditions, but the relatively few data obtained under controlled conditions of plant nutrition, such as those of Wittwer & Haseman (1945) and Dahms (1947), indicate a fruitful field for future study. There is less information relating to the response of leaf-eating insects with biting mouthparts than there is concerning those with piercing and sucking mouthparts.

Hill (1946) has made use of egg-laying rates to assess the food value of plants. He found significant fluctuations in the egg-production of *Epitrix tuberis* Gentner by alternating a diet of potato leaves with diets of plants which he had previously shown to be less favourable. With this method, however, care must be taken to distinguish between nutritional and non-nutritional effects, since oviposition may also be influenced by the colour, texture and hairiness of the plant. Nevertheless, these factors should be of less importance in cases where the experimental diets are composed of the same variety of plant grown under different conditions of mineral nutrition, than when different types of plant are compared. Thus, the results of Smith & Northcott (1951), who fed the grasshopper, *Melanoplus mexicanus mexicanus* (Sauss.), on diets of wheat grown in sand culture at three levels of nitrogen, would appear to indicate the direct food value of each diet. These workers found that the survival and egg-production of the grasshoppers were positively correlated with the nitrogen content of the plants.

In the present paper, a study has been made of the egg-laying rates of *Phaedon cochleariae* (F.) (the Mustard Beetle) when fed on watercress leaves deficient in nitrogen, phosphorus, potassium or iron, as compared with the rate on a diet of leaves from plants grown in a complete nutrient solution.

Method.

Watercress plants (*Nasturtium officinale*) were grown under glass in water cultures. The composition of the complete nutrient solutions used were as follows:—

	Expts. 1 & 2	Expt. 3
$Ca(NO_3)_2.4H_2O$	0·33 gm. per litre	0·50 gm. per litre
$NaNO_3$	0·24 ,, ,, ,,	——
$MgSO_4.7H_2O$	0·08 ,, ,, ,,	0·09 ,, ,, ,,
KH_2PO_4	0·17 ,, ,, ,,	0·13 ,, ,, ,,
$FeCl_3.6H_2O$	0·013 ,, ,, ,,	0·016 ,, ,, ,,

By substitution in these solutions of Na for K, of Cl for NO_3, of Cl for PO_4, or by omission of Fe, characteristic symptoms of deficiency of K, N, P or Fe were readily developed. Such deficiency symptoms appeared within two or three weeks, and after this time leaves were removed as required for the experimental diets.

The beetles were caged in pairs (male and female) in 3″ × 1″ specimen tubes ventilated by means of a muslin-covered hole in the cork. The detached leaves were placed in the tubes on a small pad of damp cotton-wool. Owing to the difficulty of sexing the beetles on morphological characters, pairs were isolated while copulating. Fresh food was given every one or two days, when the eggs were counted and removed.

In each experiment, the effect on the beetles of changing the diet from mineral-deficient to complete nutrient has been studied. By this means the figures for egg-production by each female on a mineral-deficient and on the "complete nutrient" diet can be directly compared. Since a natural decline in egg-production might be expected in an experiment lasting for several weeks, the diets of mineral-deficient leaves were, in most cases, given first and were followed by diets of complete nutrient leaves. Any adverse effect produced by the mineral-deficient leaves would therefore not be enhanced by an effect resulting from increased age. In experiments 2 and 3 the diets were given in the reverse order, *i.e.*, complete nutrient leaves in the first period and mineral-deficient leaves in the second.

Experiments 1 and 2 were carried out in the laboratory during the summer, but no attempt was made to control light and temperature. In the third experiment a glass-fronted incubator was used, and light, temperature and humidity were controlled.

Results.

Experiment 1.

Three separate groups of beetles were fed for 14 days on watercress leaves deficient in phosphorus, potassium and iron respectively, followed by a diet of complete-nutrient leaves for a further 14 days. Eggs were counted every two days. The data are summarised in Table I. In estimating differences in egg-production, it has been assumed that four days must elapse before the beetles could show a complete response to a change of diet. The figures in Table I indicate that this period may, in fact, have been less than four days.

TABLE I.

The effect of phosphorus-, potassium- and iron-deficient watercress on egg-production.

No. of beetles	Diet	Period (days)	Total egg-production	Mean no. eggs per beetle	Difference of means	Diffs. signif. at 5% level
12	Phosphorus-deficient	0–4	107		10·7±3·3	7·3
		5–14	42	3·5		
	Complete-nutrient	15–18	64			
		19–28	170	14·2		
10	Potassium-deficient	0–4	50		14·4±5·4	12·2
		5–14	61	6·1		
	Complete-nutrient	15–18	89			
		19–28	205	20·5		
11	Iron-deficient	0–4	44		18·0±3·8	8·5
		5–14	7	0·6		
	Complete-nutrient	15–18	78			
		19–28	205	18·6		

Table I shows that in each case the number of eggs laid on the mineral-deficient diets was significantly lower than the number laid on a diet of complete-nutrient leaves.

Experiment 2.

Two further groups of beetles were used to test the effect of a diet of nitrogen-deficient leaves. The first group was supplied with nitrogen-deficient leaves for the first 14 days of the experiment followed by complete-nutrient leaves for a further 14 days. The second group received similar diets but in the reverse order. The data are summarised in Table II and, as in experiment 1, the figures for the first four days on each diet have been omitted in comparing treatment differences.

TABLE II.

The effect of nitrogen-deficient watercress on egg-production.

No. of beetles	Diet	Period (days)	Total egg-production	Mean no. eggs per beetle	Difference of means	Diffs. signif. at 5% level
9	Nitrogen-deficient	0–4	54		23·5±11·6	Not significant
		5–14	110	12·2		
	Complete-nutrient	15–18	64			
		19–28	321	35·7		
9	Complete-nutrient	0–4	60		22·5±5·3	18·7
		5–14	280	31·1		
	Nitrogen-deficient	15–18	42			
		19–28	77	8·6		

The total number of eggs laid in each two-day period by each group of beetles is shown in fig. 1. Although marked fluctuations in egg-production occurred

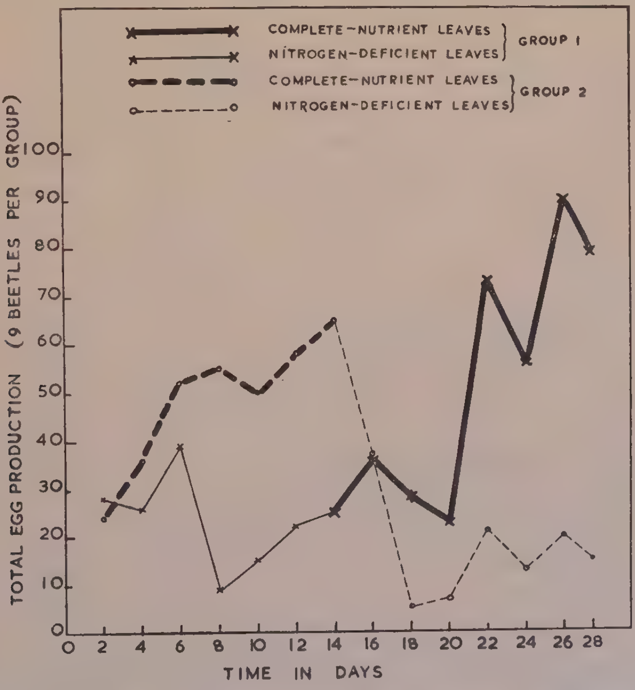


Fig. 1.—The effect of nitrogen-deficient watercress on egg-production.

during periods in which the diet was unchanged, it will be clear from the graph that there was a marked response to the change of diet in both groups.

Experiment 3.

Environmental conditions in this experiment were as follows:—

(1) Light: intensity of 22 foot-candles for 16 hours per day provided by two 25-watt tungsten lamps.
(2) Temperature: 23°C.
(3) Relative humidity: 85–90 per cent.

Two groups of beetles were used. The first group was fed for 11 days on iron-deficient leaves, followed by 11 days on a diet of complete-nutrient leaves, while the second group received similar diets in the reverse order. Leaves were changed and eggs counted every 24 hours.

The total daily egg-production for the two groups of beetles is summarised graphically in fig. 2. It is clear that the response to a change of diet was well marked after two days.

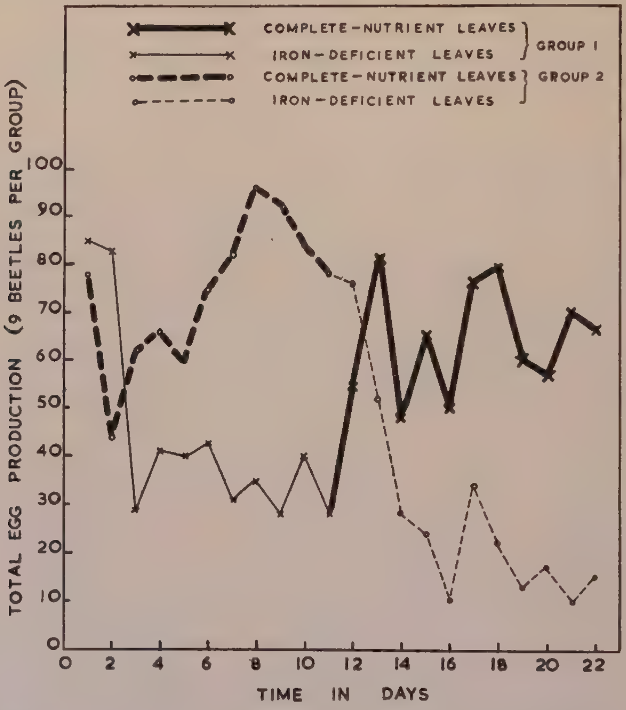


Fig. 2.—The effect of iron-deficient watercress on egg-production.

In assessing the statistical significance of the nutritional change in this experiment, therefore, only the first two days on a new diet were regarded as the transitional period. The data are summarised in Table III.

Thus, in both groups the total number of eggs laid whilst on an iron-deficient diet was significantly lower than the number produced when the beetles received a complete-nutrient diet.

Discussion.

No chemical analyses were made of the leaves used in these experiments. It is, however, of interest to note that deficiency of nitrogen or phosphorus in plants may lead to a failure of protein synthesis, of potassium to protein breakdown, and in the case of iron to a decreased absorption of nitrogen and hence to a reduced protein content of the plant. The carbohydrate content of leaves, however, may be *increased* by nitrogen-deficiency, but *decreased* by potassium- or iron-deficiency. It is possible, therefore, that the rate of egg-production may be simply related to intake of proteins.

TABLE III.

The effect of iron-deficient watercress on egg-production (controlled environmental conditions).

No. of beetles	Diet	Period (days)	Total egg-production	Mean no. eggs per beetle	Difference of means	Diffs. signif. at 5% level
9	Iron-deficient	0–2	168	35·0	28·4±9·6	22·1
		3–11	315			
	Complete-nutrient	12–13	136	63·4		
		14–22	571			
9	Complete-nutrient	0–2	122	77·2	58·0±9·6	22·1
		3–11	695			
	Iron-deficient	12–13	128	19·2		
		14–22	173			

Summary.

Studies have been made of the effect of feeding adults of the Mustard Beetle, *Phaedon cochleariae* (F.), on diets of watercress leaves (*Nasturtium officinale*) taken from plants grown in water cultures of known nutrient composition.

Significant reductions in egg-production were recorded when individual beetles were supplied with leaves deficient in nitrogen, phosphorus, potassium or iron, as compared with the egg-production of the same beetles supplied with leaves from plants grown in complete-nutrient solution.

A marked alteration in the rate of egg-production occurred within two or three days of changing the diet from " complete-nutrient " leaves to mineral-deficient leaves or *vice versa*.

References.

Dahms, R. G. (1947). Oviposition and longevity of Chinch Bugs on seedlings growing in nutrient solutions.—J. econ. Ent., **40,** pp. 841–845.

Hill, R. E. (1946). Influence of food plants on fecundity, larval development and abundance of the tuber flea beetle in Nebraska.—Res. Bull. Neb. agric. Exp. Sta., no. 143, 16 pp.

Painter, R. H. (1951). Insect resistance in crop plants.—520 pp. New York, Macmillan.

Smith, D. S. & Northcott, F. E. (1951). The effects on the grasshopper, *Melanoplus mexicanus mexicanus* (Sauss.) (Orthoptera: Acrididae), of varying the nitrogen content in its food plant.—Canad. J. Zool., **29,** pp. 297–304.

Wittwer, S. H. & Haseman, L. (1945). Soil nitrogen and thrips injury on spinach.—J. econ. Ent., **38,** pp. 615–617.

THE INSECT FAUNA OF AN EMPTY GRANARY.

By C. W. Coombs, M.Sc., F.R.E.S.
Pest Infestation Laboratory, Slough, Bucks.

and

J. A. Freeman, B.Sc., Ph.D., A.R.C.Sc.
Ministry of Agriculture, Fisheries and Food, Infestation Control Division.

(Plates XIII to XIV.)

Contents.

Description of the Granary 400
History of the Granary 400
  Detailed history 400
  Relation of the detailed history to the residual insect population 402
Survey of the Empty Granary 404
  Sampling methods 404
  Faunal list 404
  The insect population in the wall cavities 406
  The insect population in the grain-distributor system 412
  The insect population in other areas sampled 413
Discussion 414
Summary 416
Acknowledgements 416
References 417

When infested materials are stored in a warehouse and subsequently removed, some residue, with its complement of insects, is usually left behind. This residual material may lie loosely in cracks in the floor or the walls, or may penetrate into the fabric of the building where, hidden from sight and inaccessible during normal cleaning, it acts as a breeding ground for insects carried in with it and those wandering there later. In this way populations can build up within the structure of the building and later infest goods put into store.

The major factors influencing the quantity of the residual material will be the design of the warehouse, its upkeep and the standard of hygiene observed during storage. The insect species will be determined by the type of food stored, the ability of the insects to overwinter and, if food material is scarce, the ability to survive in competition with the other species present. The residual material will change with time due to natural deterioration and insect attack, and one would expect a succession of different types of dominant insects. Subsequent introduction of more food, or new foodstuffs, might modify or alter this succession.

As a greater degree of control of the infestation of goods stored in warehouses is achieved, it is essential, if the treatment is to be more than temporary, that there should be no source of re-infestation in the building. This would necessitate the use of newly designed buildings, which is not immediately practicable, or else control of the residual populations in existing structures. This survey is, it is hoped, the first of a series designed to show what parts of warehouses harbour the most insects, and the types and numbers of insects to be expected in buildings of different construction and with different types of storage.

DESCRIPTION OF THE GRANARY.

The granary examined was situated in a dock area in the west of England and covered an area of 350 ft. × 70 ft. with its long axis running approximately north and south. There were six floors with a conveyor-belt housing above, and the capacity was 12,000 tons. The roof, which started at the fourth story, was of galvanised iron with wooden-framed skylights and there was a gap where it met the side walls. The walls had a wooden framework which was covered on the outside with galvanised-iron sheeting and lined internally with tongue-and-groove fitted timber. The floor of each story was of single thickness timber except at ground level where it was of concrete.

The granary was built in 1884, and used extensively until 1918 when the authorities built a more modern building nearby. It was not used from 1930 until 1938, when security stocks were placed in store, and from then it was used continuously until it was cleared in 1951 preparatory to demolition. The fauna of the empty granary was studied during 1951 by one author (C. W. C.) and the history was compiled and presented by the other (J. A. F.).

HISTORY OF THE GRANARY.

The warehouse was first seen in 1938 during the survey of infestation of grain (Munro, 1940). From 1942 onwards, it was visited periodically by inspectors of the Ministry. This account is based on their reports, by permission of the Ministry.

In the consideration of the origin of infestation in the granary, it should be noted that, with minor exceptions, grain taken into this granary comes from the nearby port in barges, which are filled either direct from ocean vessels or from the silos in the port. There is thus opportunity for grain, clear of infestation in the ship, to acquire infestation from the silos and the barges. It may further be noted that Canadian grain of all kinds may be assumed to be usually clear of infestation on arrival in this country, except for small numbers of mites and the occasional occurrence of *Laemophloeus* spp. Grain from other parts of the world is usually infested to a lesser or greater degree. Home-grown grain may also generally be assumed to be clear. These assumptions are made in this account of the history of the granary.

Detailed History.

The granary was seen first in October 1938, when U.S.A. hard winter wheat had been in store since mid-August. According to the granary staff this was the first time the granary had been used since 1930. The surface of the wheat was heavily infested with larvae of *Ptinus tectus* Boield. and locally there were moderate numbers of *Calandra oryzae* (L.). One adult *Plodia interpunctella* (Hb.) was seen in flight.

This grain was removed some time before June 1941, when Manitoba wheat was placed in store.

When seen in February 1942, mites, Psocids, moth larvae (unidentified) and some dead *Calandra granaria* (L.) were found. More Manitoba wheat was taken into store in June, and when seen in September the grain was heavily infested with migrating larvae of *Ephestia elutella* (Hb.). Other insects present included *P. tectus* (large numbers), few *Hofmannophila pseudospretella* (Stnt.), *Endrosis sarcitrella* (L.) and *Tenebroides mauritanicus* (L.).

The wheat was removed by April 1943, and whilst the warehouse was empty it was sprayed with 0·8 per cent. pyrethrins in oil. During May the warehouse was refilled with Manitoba wheat and home-grown barley. The latter remained in store for only a few weeks.

Inspections in March and June showed a fairly heavy infestation of *E. elutella*, and other insects present included *C. granaria*, *Tenebrio molitor* L., *Tenebroides mauritanicus*, *P. tectus*, *Ptinus fur* (L.) (dead adults only), *H. pseudospretella*, *E. sarcitrella*, *Cryptophagus* spp., *Tribolium castaneum* (Hbst.) (dead adults only), *Rhizopertha dominica* (F.) (dead adults only) and the mite, *Tyroglyphus farinae* (Deg.).

Although the wheat was sprayed at frequent intervals with 0·8 per cent. pyrethrins in oil, a considerable infestation of moth larvae (*Ephestia elutella*) developed in it, the earliest migration taking place on the top floor at the end of July.

Other insects seen on the grain or in the granary during the summer were *Laemophloeus* sp. (in August), *Plodia interpunctella* (October) (adults and larvae locally on the top floor only) and *Tinea granella* (L.) (August). At the end of the year there was a fair population of larvae of *E. elutella* (spun up in the fabric of the building), small numbers of *C. granaria*, *T. molitor*, *Tenebroides mauritanicus* and large numbers locally of *Tyroglyphus farinae*. Bagged home-grown barley was taken into store in November.

The warehouse was inspected thoroughly in March and April 1944 and small numbers of larvae of *E. elutella* were found in cracks and sheltered parts of the granary. Associated with rotting grain and dust in corners in cracks and crevices were moderate numbers of *H. pseudospretella* (larvae), *Endrosis sarcitrella* (larvae), *Ptinus* spp. (larvae—probably both *P. tectus* and *P. fur*), *T. molitor* (larvae), Psocids and mites (*Tyroglyphus farinae*). Insects found only dead were *Lyctocoris campestris* (F.), *Cryptophagus* sp., *Calandra granaria*, *Tribolium castaneum* and *Tenebroides mauritanicus*.

The Manitoba wheat was sprayed regularly during the summer and early autumn with 0·8 per cent. pyrethrins in oil and sticky banding was applied in August. Despite the spraying, *Ephestia elutella* bred in the wheat and there were large migrations from the end of August onwards. During the summer *C. granaria* was observed in small numbers at each inspection.

In January 1945 the granary had fair numbers of *Ephestia elutella* (larvae), few *Tenebrio molitor* (larvae), *C. granaria*, *Tenebroides mauritanicus*, *Attagenus pellio* (L.) (larvae), *P. tectus*, *P. fur*, *H. pseudospretella* (larvae), *Endrosis sarcitrella* (larvae), *Tribolium castaneum* (dead adults) and mites (*Tyroglyphus farinae*).

The stock of wheat which had been in store since 1943 began to go out in April 1945, and new wheat was taken in from July onwards. As in previous years, the wheat in the granary was sprayed at frequent intervals during the summer but there was again some attack by *E. elutella*. In September, heating was discovered in the old stock of Manitoba wheat on the fourth floor, *C. granaria* and *Laemophloeus* spp. being present in the heating grain. In November, further heating occurred in the old stock on the ground floor associated with *C. granaria*, *Laemophloeus* and *Oryzaephilus surinamensis* (L.). The latter species had been recorded in the granary for the first time in June (when several dead adults were found) before the new stock of wheat had started to come in.

The grain was delivered fairly rapidly and the granary was completely empty by March 1946. Infestation, mainly found on the ground floor which had not yet been cleaned, was by *E. elutella* (larvae in fabric), *C. granaria*, *O. surinamensis*, *T. molitor*, *P. tectus*, *Enicmus minutus* (L.), *Cryptophagus* spp., and *A. pellio*.

Much the same infestation was found in July when the wall linings of the ground floor were being repaired.

Before grain was put in store in June 1947, the granary was sprayed with 0·8 per cent. pyrethrins in oil. Canadian oats and Amber Durum wheat were taken into store from June to November.

When seen in March 1948, there was a general moderate to heavy infestation of *C. granaria*, *C. oryzae*, *O. surinamensis*, *Laemophloeus* spp., other insects present being *P. tectus*, Psocids and *R. dominica* (dead) and mites, *T. farinae*.

From July onwards the Canadian oats were delivered (the wheat had gone out in April) and were replaced by Russian oats and barley and Australian oats, which were known to be infested.

Although the particular shipments of Russian barley and oats were not inspected, other cargoes of Russian barley and oats arriving at about the same time showed light infestation of *C. oryzae*, *C. granaria*, *O. surinamensis*, *Laemophloeus* spp. and mites.

Inspection of the Australian oats in the ship showed *C. granaria*, *O. surinamensis*, *Laemophloeus*, *R. dominica*, Psocids and *Cryptophagus* sp., on this parcel. Other shipments had also *Calandra oryzae*.

Australian wheat arriving in the country at this time was infested with *C. granaria*, *C. oryzae*, *Ephestia cautella* (Wlk.), *Laemophloeus* spp., *O. surinamensis*, *R. dominica*, *Sitotroga cerealella* (Ol.) and *T. castaneum*.

The Russian oats and barley rapidly showed heavy infestation and heating with *C. granaria*, *C. oryzae*, *Laemophloeus* and *O. surinamensis* and several parcels were removed from the granary, fumigated in barges using methyl bromide, and then replaced in the granary. Some of this infestation may have been acquired from the Canadian oats.

E. elutella bred again in the stocks of grain during the year. An insect observed in the granary for the first time was *Tipnus unicolor* (Pill. & Mitt.).

Measures of control other than fumigation were the use of gamma BHC sprays and dusts, the latter used particularly as barriers between different piles of grain. Similar measures were used in 1949.

In January 1949, infested Plate maize was taken into store on the fourth floor. In the ship it had been found infested with *C. oryzae*, *O. surinamensis*, *T. castaneum*, *Laemophloeus* spp., *E. cautella* and *S. cerealella*. Although *Rhizopertha* and *Plodia* were not recorded on these parcels they were found regularly in other Plate maize arriving in this country at that time. In the course of the year in the granary it became heavily infested with *C. oryzae*, *C. granaria*, *R. dominica*. *T. castaneum*, *S. cerealella*, *Laemophloeus* spp. and *P. interpunctella*. Australian wheat (infested) (taken in during April) and Manitoba wheat (taken in during August) also became infested mainly by movement of insects from the already infested oats and maize.

Early in 1950 all grain except Manitoba wheat had been delivered and during that year the insect population remained fairly steady at *E. elutella*, *C. granaria*, *O. surinamensis*, *Laemophloeus*, *Tenebroides mauritanicus*, *P. tectus* and *Tribolium castaneum*. It would seem that the *C. oryzae* and *S. cerealella* were killed by exposure to winter conditions.

When the warehouse was finally seen in March 1951, when it was nearly empty, the infestation found was by *E. elutella* (larvae), *C. granaria*, *O. surinamensis*, *Laemophloeus* spp., *Tenebrio molitor*, *Tenebroides mauritanicus*, *P. tectus*, *Trigonogenius globulus* Sol., *Cryptophagus* spp., Psocids, *Tribolium castaneum* and mites (*Tyroglyphus farinae*).

Relation of the detailed History to the residual Insect Population.

It is possible to list certain species as being clearly established in the warehouse, and to have survived for the whole period under review. They may have been added to from time to time but there is no evidence that they would have died out if no further introductions had been made. The major species are the following:—

Calandra granaria—dead in February 1939, living from June 1943 onwards.

Ephestia elutella—probably introduced from port granaries with the first parcels of Canadian wheat. First recorded September 1942, but the larvae referred to in report of February 1942 may have been of this species.

Tenebrio molitor—March 1943 onwards.

Tenebroides mauritanicus—September 1942 onwards.

Ptinus tectus—October 1938 onwards (clearly established for many years previously).

Psocids—October 1938 onwards.

Hofmannophila pseudospretella and *Endrosis sarcitrella*—September 1942 onwards.

Tyroglyphus farinae—February 1942 onwards.

In a second group are species which became established at an intermediate stage in the period under review.

Laemophloeus sp.—there is a solitary record in August 1943, and not again until September 1945, when it was found in association with *C. granaria* and *O. surinamensis* in the old stock Manitoba. It was probably brought in originally in that wheat (it has been recorded fairly regularly in Canadian wheat) and took a long time to breed up. It may have kept going in cracks and re-appeared in March 1948, when it broke out in the oats. One cannot exclude further introduction. From then on it can be regarded as an established pest. In the absence of identification to species it is difficult to draw firm conclusions.

Oryzaephilus surinamensis—first recorded in June 1945 (dead) in the Manitoba wheat stored since 1943, before the introduction of new wheat. It was frequently recorded from then onwards. It may have originally been introduced with the 1943 Manitoba and taken a long time to breed up. Was probably re-introduced with the Russian or Australian grain.

The remaining species differ among themselves in their ability to persist in such situations, but in this instance all seem to have depended on periodical re-introduction.

Plodia interpunctella—present in October 1938: slight outbreak in October 1943. May have been introduced with the grain in the same way as *Ephestia*. *Plodia* is known to have been present in the port granaries. Did not occur again until October–November 1949, when it was associated with the infestation on the Plate maize and was probably introduced with it.

Calandra oryzae—present in October 1938, in U.S.A. hard winter wheat, a commodity in which it is known to occur on import. Next occurred in March 1948 in Canadian oats. One would not expect this species in such grain on import and it may have been introduced from an infested barge or other source outside the warehouse. Also introduced on Plate, Australian and Russian grain. Winter conditions in 1949–50 probably killed it off.

Rhizopertha dominica—the original discovery in June–July 1943 (all dead) must have been residual from a long time previously. The same applies to the discovery in March 1948. Outbreaks in the Plate maize in October–November 1949 were due to introduction with the grain.

Tribolium castaneum—dead only from June 1943. Introduced in January 1949 with Plate maize and managed to survive the winter, probably protected in the Manitoba wheat. In the absence of heating it would not establish itself permanently.

Survey of the empty Granary.

Sampling Methods.

The chief aim of the investigation was to discover the kinds and numbers of insects present which would not be found during a routine superficial inspection of the building. The most likely places in this granary were the cavities between the internal and external facings of the walls and parts of the grain distributor system.

Walls.

The wall cavities were examined in greatest detail. The structure of all the walls was essentially similar, with a number of partially sealed compartments along each wall on every floor. Each compartment (Pl. XIII, fig. 1) was approximately 9 ft. long and was subdivided by secondary supports. Either a whole or a half of one of these main compartments of the end walls on each floor was chosen at random and exposed for sampling, and a quarter of such a compartment exposed on the side walls. Sealing boards were removed from above and below and the timber wall lining was forced free with a case opener. The boards removed in this way were scraped, the tongue-and-groove fittings were cleaned and all the débris collected and bottled. The cavities were brushed clean and all residues collected and brought to the laboratory for examination.

Distributor system.

Certain parts were dismantled, the boards scraped, and the residues found beneath the metal linings of the chutes were collected.

Other areas.

Collections of residues were taken from the top of the walls on the fourth floor and from the eaves which formed a ledge outside the tops of the walls on the fourth floor. The stairs on this floor were partially dismantled and the boards cleaned. All the dust and grain between the boards was collected.

The material brought to the laboratory was sieved and placed upon heated trays from which the insects were collected. Due to the method of examination the inactive stages of all species, the larvae of *C. granaria*, and other small larvae were not collected. The webbing and scrapings from the boards were examined separately and moth and other larvae counted.

Faunal List.

THYSANURA
  Unidentified

PSOCOPTERA
  Unidentified

HEMIPTERA
  Anthocoridae
    Lyctocoris campestris (F.)
  Reduviidae
    Empicoris culiciformis (Deg.)

LEPIDOPTERA
  Oecophoridae
    Hofmannophila pseudospretella (Stnt.)
  Tineidae
    Tinea pallescentella Stnt.
  Pyralidae
    Pyralis farinalis (L.)
  Phycitidae
    Ephestia elutella (Hb.)

COLEOPTERA
  Staphylinidae
    Unidentified
  Ptinidae
    Ptinus tectus Boield.

COLEOPTERA—*continued*
- Dermestidae
  - *Attagenus pellio* (L.)
- Trogositidae
  - *Tenebroides mauritanicus* (L.)
- Cucujidae
  - *Oryzaephilus surinamensis* (L.)
  - *Laemophloeus minutus* (Ol.)
- Cryptophagidae
  - *Cryptophagus saginatus* Sturm
  - *Cryptophagus cellaris* (Scop.)
  - *Cryptophagus pilosus* Gylh.
  - *Cryptophagus distinguendus* Sturm
  - *Cryptophagus obsoletus* Rter.
  - *Ptinus fur* (L.)
  - *Ptinus pusillus* Sturm
- Tenebrionidae
  - *Tenebrio molitor* L.
- Curculionidae
  - *Calandra granaria* (L.)

HYMENOPTERA
- Unidentified

DIPTERA
- Scenopinidae
  - *Scenopinus fenestralis* (L.)

SIPHONAPTERA
- Ceratophyllidae
  - *Nosopsyllus* sp.

ACARINA, ARANEIDA, PSEUDOSCORPIONIDA, ISOPODA

Species of which dead specimens only were found were:—

COLEOPTERA
- *Laemophloeus ferrugineus* (Steph.)
- *Anobium punctatum* (Deg.)
- *Lyctus brunneus* (Steph.)
- *Corticaria fulva* (Comolli)
- *Lathridius bergrothi* Rter.
- *Typhaea stercorea* (L.)
- *Mycetophagus quadriguttatus* Mueller
- *Rhizopertha dominica* (F.)
- *Latheticus oryzae* Waterh.
- *Tribolium castaneum* (Hbst.)
- *Calandra oryzae* (L.)

Species reported as present in the granary at some time between 1938–51, but not included above were:—

LEPIDOPTERA
- Gelechiidae
  - *Sitotroga cerealella* (Ol.)
- Oecophoridae
  - *Endrosis sarcitrella* (L.)
- Tineidae
  - *Tinea granella* (L.)
- Phycitidae
  - *Plodia interpunctella* (Hb.)
  - *Ephestia cautella* (Wlk.)

COLEOPTERA
- Lathridiidae
  - *Enicmus minutus* (L.)
- Ptinidae
  - *Trigonogenius globulus* Sol.
  - *Tipnus unicolor* (Pill. & Mitt.)

The only insect species which had not previously been found associated with stored products in England was *Cryptophagus obsoletus*. This species was found in the wall cavity on the ground floor of the south wall where it was associated with a large population of *C. saginatus*. It is reported (Bruce, 1936) as being a Siberian species which has spread to Russia, and its presence in this granary was possibly due to a consignment of infested Russian oats stored in 1948. Further investigation has shown the species to be established in England (Coombs & Woodroffe, 1952).

The Insect Population in the Wall Cavities.

Number of insects.

Most of the insects found were living in the residues within the cavities rather than on or between the boards removed, and, as these residues were found on the horizontal beams, the height of the wall (which varied between floors) was not an important factor governing the numbers of insects present. The width of the cavities was always that of the supporting beams and did not vary. Therefore, when reducing the sample cavities to units for comparison only the length of the sample has been used, and the figures are expressed as numbers of insects behind one foot of wall (Table I).

TABLE I.

The number of insects found per foot of wall cavity.

Wall / Floor	North	South	East	West	Mean
5	4	4	—*	—*	4
4	68	32	4	53	39
3	91	270	20	16	99
2	353	647	2	44	262
1	649	576	3	158	347
G	2,266	799	22	297	846
Mean	572	388	10	113	266

* The fifth floor had no double side walls because the slope of the roof extended to the fourth floor.

The shorter end walls (north and south) supported greater populations than the side walls and there was a general tendency for the number of insects to increase towards the ground floor, especially on those walls where the populations were more dense.

When the débris was examined in the laboratory a rough check upon its quality and quantity was made. The quantity was measured by volume, using arbitrary units. When the population densities are expressed as numbers of insects per unit volume of débris, the contrast between the different walls and the tendency to increase towards the ground floor are greatly reduced (Table II).

The quality of the débris collected varied from a fine coal dust (derived from the adjacent railway sidings) to large quantities of grain in good condition. Four rough groupings for quality were made:—

(1) Residues containing a high proportion of whole grain.
(2) Ground-floor residues with whole grain less concentrated and much of the remaining material composed of glumes (barley and oats had been stored on this floor), and general detritus.
(3) Residues with a low concentration of whole grains and the bulk of material a floury powder, dust and grit.
(4) Residues with very few or no grains and made up mainly of dust and grit.

The proportion of whole grains, in general, increased with the volume of the residues, and the dirt, floury powder, and grit were still found when there were many grains. The residues in Group 1, therefore, contained not only the best quality of wheat grains but also the most varied supply of food material. The effect of the varying quality of the residues upon the number of insects found is shown in Table III, where the average number of insects supported reflects the quality of the residue. Group 2, consisting of all ground-floor residues examined, is a rather specialised grouping in that the number of insects found is in part due to the special conditions found there; these areas were the dampest of all examined, and all the Staphylinids and the bulk of the Cryptophagids were found here. The figure for this type of residue is therefore probably a little higher than it should be relative to the others in the Table.

TABLE II.

The number of insects per unit volume of débris in the wall cavities.

Wall / Floor	North	South	East	West	Mean
5	2	4	—	—	3
4	34	16	9	7	17
3	13	45	3	5	17
2	177	50	1	7	59
1	54	30	1	39	31
G	49	12	1	49	28
Mean	55	26	3	21	26

Thus the total numbers of insects present per unit length of wall depended largely upon the volume and the quality of the débris present. It happened in this building that more food was present in the wall cavities of the lower floors and so the numbers of insects per unit length were less on the upper stories. After variation due to volume and quality of food material has been eliminated

TABLE III.

The number of insects found in residues of different food quality.

Group	Number of cavities	Average number of insects
1	8	52·4
2	4	28·0
3	5	12·3
4	5	1·9

For description of the grouping see text.

there remains a difference between walls and between different floors of each wall probably due to the physical factors of the environment (temperature, humidity), infestation of commodities stored nearby, and the condition of the wall boards.

Composition of the fauna.

Comparison between the different levels of the walls.—It has been seen that both the number of insects and the amount of residue increased on descending the granary. This same trend was shown by the number of species present in any area and, in some cases, by the number of individuals in any one species. Table IV shows the increase in number within species on descending the granary. The trend is more marked in some species than in others: the ones showing it least were *A. pellio*, *Tenebroides mauritanicus*, *E. elutella*, *Ptinus* spp. and *S. fenestralis*; those showing it most markedly were *C. granaria*, *H. pseudospretella* and *Tenebrio molitor* (fig. 1). *A. pellio* was found in areas where the residues were mainly dirt and dust and where many of the other species found in the granary could not exist. As the quantity and the quality of the food materials increased the population of *A. pellio* did not increase proportionately. *T. mauritanicus* also showed little increase in numbers as the amount of food increased, possibly because its ability to feed upon other species (Candura, 1932) helped to maintain its numbers when the food supply was reduced.

TABLE IV.

The numbers of individuals of the main species found per foot of wall cavity on each floor.

Floor / Species	G	1	2	3	4	5
**C. granaria* ..	174	81	117	59	5	—
**O. surinamensis* ..	12	24	2	—	—	—
T. molitor ..	119	35	64	8	6	—
Ptinus spp. ..	13	17	11	2	3	2
A. pellio ..	7	18	1	2	3	—
T. mauritanicus ..	1	3	4	1	2	—
H. pseudospretella ..	413	146	51	5	2	1
E. elutella ..	1	17	9	2	12	1
S. fenestralis ..	11	2	2	9	4	—
*Hymenoptera ..	9	4	—	—	—	—
**Cryptophagus* spp. ..	74	—	—	—	—	—
*Staphylinidae ..	8	—	—	—	—	—

* Only adult stage counted.

The figures represent mean values of all four walls except on the fifth floor, where no double side walls were present and only results from the end (north and south) walls are used.

At the other extreme, the number of individuals of *C. granaria* (which needs whole grain for its development) increased markedly with increase in food. The number of *H. pseudospretella* also increased, but here the number of whole grains present was not important and the cause was probably the actual increase in volume. In general, throughout the granary, when the volume of residue increased there was also an increase in the number of whole grains. Another important factor running parallel to increase in volume of residue was the humidity, which increased as the ground level was reached. The most marked concentration of *H. pseudospretella* was 1,000 larvae per foot of wall on the ground floor where residues were very damp. Other insects limited by humidity were the

Staphylinids and the various *Cryptophagus* species which were found mainly on the ground floor.

Comparison between the north and south walls.—The volume and quality of the food material behind these walls were similar and large insect populations were found. The dominant species were *H. pseudospretella* in the cavities of the north wall and *C. granaria* in the cavities of the south wall. *H. pseudospretella* was present in only very small numbers in the south wall, but *C. granaria* was well represented in the north wall. The only obvious difference between the two walls was in their position relative to the sun. The walls were covered with galvanised-iron sheeting and even in April, when this survey was carried out, it was noted that the cavities in the south wall heated up considerably on sunny days. The mean temperature of the south wall cavities would thus be higher and the grain would be correspondingly drier. As *H. pseudospretella* requires a high humidity for development and temperatures over 25°C. are adverse (Woodroffe, 1951), these physical conditions may have precluded its presence in large numbers in the south wall. That the two species are not mutually exclusive was shown in the north wall cavities where, although *H. pseudospretella*

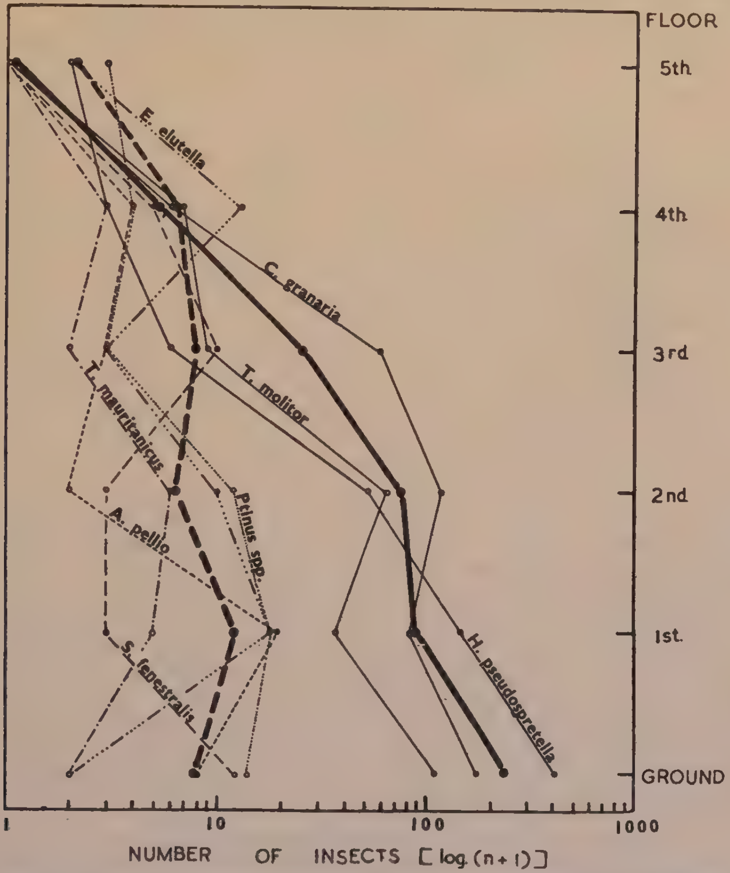


Fig. 1.—The number of insects found per foot of wall cavity on each floor.
Broken lines: species showing little or no increase in the lower parts of the granary.
Unbroken lines: species showing a marked increase.
The mean of each group is shown by a heavy line.

predominated, *C. granaria* was also present (Table V). The very high figure for *H. pseudospretella* on the north wall was mainly due to a very dense population on the ground floor where conditions were very moist and where approximately 1,600 larvae were found per foot of wall cavity examined. Other species were present as shown in Table V.

TABLE V.

The average number of insects per foot of wall cavity in each wall.

Wall Species	North	South	East	West
**C. granaria*	53	214	1	28
**O. surinamensis*	—	25	—	—
T. molitor	68	54	4	34
Ptinus spp.	10	11	1	14
A. pellio	6	1	2	15
T. mauritanicus	3	4	—	2
H. pseudospretella	406	3	1	3
E. elutella	12	7	—	12
S. fenestralis	8	5	2	5
*Hymenoptera	6	3	—	—
**Cryptophagus* spp.	1	49	—	—
Staphylinidae	—	5	—	—

* Only adult stage counted.

Comparison between the east and west walls.—The west wall harboured more food and insects than the east wall, but both contained smaller residues than the end walls and those present were usually in a bad condition with a high proportion of inedible material. Owing to this reduction in food quality the major grain pests were less important components of the fauna. *T. molitor* and *C. granaria* are listed as dominant on the west wall, and *T. molitor* on the east wall, but in both cases this was due to the presence of large quantities of material on the ground floor with correspondingly large numbers of these species. If dominance due to a single large population in any part correlated with large deposits of food is ignored, a clearer pattern of distribution is seen. On the west wall *A. pellio*, *Ptinus* spp., *E. elutella*, and *S. fenestralis* were predominant, while on the east wall the bulk of the population consisted of *A. pellio* and *S. fenestralis*.

That the difference between the side and end walls is due mainly to the food material present and not to temperature or humidity conditions was shown on the ground floor of the west wall where the residues were similar in quality and quantity to those found in the north and south walls, and where a very similar population was supported. Also, at one point on the third floor, a large amount of grain had entered the east wall through a hole made in the wall boards by rats. Here again the population was similar to that found in comparable cavities of the end walls with *C. granaria* (45% of the population), *Tenebroides mauritanicus* (26·6%) *Ptinus* spp. (11%) and *Tenebrio molitor* (9·5%) forming the bulk of the population.

The composition of the fauna over all sample areas.—The general distribution of insects over the four walls showed a change in dominant species correlated with a change in the condition of residues. The vertical distribution of residues in the wall cavities obscures the differences between the walls because the lower floors of the side walls have larger deposits than the upper floors of the end walls. The sample wall cavities can be arranged in a series, regardless of location, according to the total numbers of insects supported by a unit volume of food

(Table VI). In this way the change in importance of the various species with a decrease in the capacity of the residues to support large populations is seen. (The number of insects supported per unit volume of food has been shown to correspond roughly to the quality of the food and here is used as an index of food quality.) Where the food was of the best quality, with many whole grains, *C. granaria* and *H. pseudospretella* were present in large numbers, and one or the other dominated the fauna. As the food quality deteriorated the numbers of both species fell rapidly and they became negligible components of the population (fig. 2).

TABLE VI.

The change in importance of various species with decreasing numbers of insects per unit volume of residue in the wall cavities.

Number of insects per unit volume	41+ (Av. 70·7)		40–11 (Av. 24·2)		10–2 (Av. 4·8)		1–0 (Av. 0·9)	
Number of areas in the group	6		6		6		4	
Species	Average number	% of population	Average number	% of population	Average number	% of population	Average number	% of population
C. granaria ..	20·84	35·0	6·49	32·5	0·10	3·2	—	—
H. pseudospretella	29·63	36·0	0·87	4·5	0·61	13·1	0·01	—
Ptinus spp. ..	0·97	1·9	2·20	6·0	1·14	23·8	0·09	9·7
A. pellio ..	0·56	0·9	2·77	7·9	0·45	8·5	0·54	58·6
S. fenestralis ..	1·02	1·5	1·11	6·0	0·70	15·3	0·17	18·0

The numbers of insects are an index of the quality of the food residues.

The numbers of *Ptinus* spp. increased slightly and then fell; more noticeable was the change in importance of the genus at a concentration of between 2 and 10 insects per unit volume where it rose to represent 23·8 per cent. of the total population. The numbers of *S. fenestralis* were never high, but as they fell off relatively slowly the species increased in importance as a constituent of the population where food quality was bad. The numbers of *A. pellio* fluctuated but showed no trend in either direction so that when only few insects were found it represented the majority of the population (58·6%). Often where little food material was present in the residues only *A. pellio* and *S. fenestralis* were found.

Thus when many whole grains were present in the residues *C. granaria* was found in large numbers. As the ratio of whole grains to floury dust decreased *Ptinus* spp. increased in importance until the amount of inedible and contaminated materials caused the decrease seen at the lowest concentrations. Finally, only *A. pellio* and *S. fenestralis* were found. The former is often found lingering in such situations after other species have disappeared, and this, no doubt, is due to its scavenging habits and long larval life. *S. fenestralis* is a predator and its presence may be due to the usual predator-prey time lag.

The succession of dominant insects indicated by these observations would seem to be *C. granaria* (either accompanied or partially replaced by *H. pseudospretella* when there is a sufficiently high humidity) when there are large amounts of residues with whole grains and dust, followed by *Ptinus* spp. as the food material becomes less and whole grains are broken down, and finally *A. pellio* which, together with *S. fenestralis*, usually outlasts all other species. *T. molitor* was found in all classes of residue and showed a general decrease in numbers as the food deteriorated. *O. surinamensis*, when found, was always present as a subsidiary to *C. granaria*. *E. elutella* was found sporadically throughout the building irrespective of food conditions within the cavities.

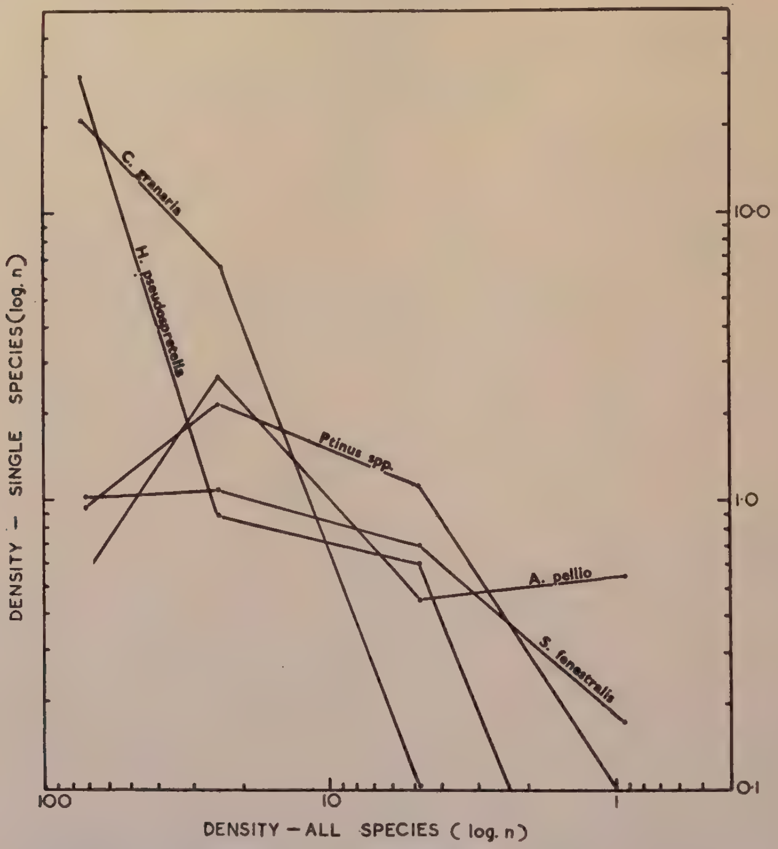


Fig. 2.—The relationship between the abundance of certain species and the total insect population (this total is taken as an index of the quality of the residue).

The Insect Population in the Grain-distributor System.

From a conveyor belt above the fifth floor, 32 conveyors took grain down into the middle parts of all floors and the same number passed out obliquely, alternately to right and left, along the length of the warehouse to the fourth floor, and from there vertically to ground level, to supply the sides. There were thus three rows of delivery chutes on each floor, the middle row with 32, and the side rows with 16 each.

Three parts of the system were chosen at random for examination; an oblique chute on the fifth floor, one on the opposite side on the fourth, and a vertical distributor on the second. As the chutes were in continual use little débris accumulated in them, but, even so, grain and floury dust were found in cracks in the woodwork and lying beneath the sheet metal which lined the inside of the oblique chutes.

From the chute examined on the fifth floor very few *C. granaria* or *H. pseudospretella* were found. The dominant insect was *E. elutella* (127 individuals representing 76·8% of the population) followed by *Ptinus* spp. (11·3%), *T. molitor* (5·4%), *A. pellio* (2·4%) and Hymenoptera (2·4%).

The amount of residue in the chute sampled on the fourth floor was three times as much as in that on the fifth. The population was made up of *Tenebrio molitor* (184 individuals; 44·4% of the population), *Tenebroides mauritanicus* (27·1%), *Ptinus* spp. (9·7%), Hymenoptera (3·9%) and a few *A. pellio* (1·7%) and *C. granaria* (1·0%).

In the vertical chute on the second floor there was a lot of webbing but few living moth larvae were found associated with it. The population was relatively sparse, with *Tenebrio molitor* dominant (13 individuals; 56%), and including *Ptinus* spp. (21·7%), *A. pellio* (8·7%), *Tenebroides mauritanicus* (8·7%) and *O. surinamensis* (4·3%).

The type of population living in the chutes is essentially similar to that found within the cavities of the walls where the numbers of insects per unit volume is below maximum and *Ptinus* spp. are reaching their dominant phase (*cf.* Table VI). The dominant insects are *Tenebrio molitor*, *Ptinus* spp. and *Tenebroides mauritanicus*.

The Insect Population in other Areas sampled.

Top of side walls and eaves.

The slope of the roof started on the fourth floor and at the junction of wall and roof there was a space of about three inches between the eaves and wall (Pl. XIII, fig. 2). The top of the wall and the horizontal ledge of the eaves served as repositories for dust and grain blown there during the movement of stored grain. These areas support a more superficial type of residual population than that present within the walls.

On top of the west wall much dust was found, together with wheat grains in fairly good condition and a few grains of maize. The insects present in the area sampled (3′ × 9″) were *Tenebrio molitor* (163 individuals; 62·5% of the population), *Ptinus* spp. (49; 18·8%), *S. fenestralis* (26; 10%), *Tenebroides mauritanicus* (11; 4·2%), *A. pellio* (6; 2·3%), *H. pseudospretella* (5; 1·9%) and *C. granaria* (1; 0·4%). There were many dead insects, mainly *C. granaria*, *C. oryzae*, *Tribolium castaneum*, *O. surinamensis* and *Laemophloeus* spp. The residues on the east wall were sparser and composed mainly of dust and glumes with only scattered grains of wheat and barley. The species found were the same as on the west wall but the percentage composition had changed due to a reduction in importance of *Tenebrio molitor* (62·5% to 32·3%) and an increase in that of *A. pellio* (2·3 to 22·8%).

The eaves were separated from the wall by a distance of about three inches but non-flying insects would be able to cross the gap by the supporting beams. Also whole maize grains were found in the eaves, and if these could be blown there during movement of grain, insects could equally well arrive by the same agency.

On the area of the eaves examined on the west wall there was a considerable amount of dust with some wheat and maize grains, while on the east wall there were similar amounts of dust but only occasional wheat grains. The population supported on the west wall was dominated by *S. fenestralis* (46 individuals; 65·7% of the total population) with *Ptinus* spp. (17; 24·3%), *A. pellio* (3; 4·3%) and *H. pseudospretella* (3; 4·3%) also present. On the east *A. pellio* (257; 81·6%) was predominant, with *S. fenestralis* (34; 10·8%), *T. molitor* (21; 6·7%) and *Ptinus* spp. (3; 1·0%) as subsidiaries.

All these areas support populations resembling those found in the cavities of the walls with dominance passing from *T. molitor* and *Ptinus* spp. to *A. pellio* and *S. fenestralis* according to the condition of the débris.

Staircase on the fourth floor.

The stairs leading from the fourth to fifth story were placed in the middle of the floor at each end of the warehouse and were provided with side protection boards (Pl. XIV, fig. 1). Four of these boards, varying in length from 7′ 6″ to 9′ 6″, were removed, the dust and grains present between the boards collected and the moth larvae scraped from the boards. The dominant insects found were *Ptinus* spp. (42; 30%) with *E. elutella* (24; 17·1%) and *A. pellio* (19; 13·6%) as subsidiaries. Other species present were *Tenebrio molitor* (10%), *C. granaria* (10%), *Tenebroides mauritanicus* (6·4%), Hymenoptera (5%), *S. fenestralis* (4·3%) and *H. pseudospretella* (3·6%). In all, 140 individuals were found by the removal and examination of these four boards where there was little protection and where the débris just lay in the cracks. This situation must occur frequently in warehouses with wooden interiors, and these numbers suggest that fairly large populations could build up even though no infestation were possible in concealed areas. The populations in these more open situations are more likely to be affected by wandering adults and larvae than those within the wall cavities, and the results noted above are not necessarily due to a permanent population, but even so they do conform with previous results where the bulk of the residues were floury dust and wheat grains.

DISCUSSION.

The infestation of clean goods by insects already present in a warehouse has been noted on many occasions but it is doubtful if the size of the residual populations has been fully realised. The warehouse examined was admittedly of poor design, but the standard of hygiene was high, and the conditions were probably not exceptional for this type of construction. Elimination of the double walls would have removed a large part of the population, but the distributor system and cracks would have supported populations large enough to form loci for major infestations, if the few samples taken are indicative of the general conditions.

Most of the pests that were introduced into the granary became incorporated into the residual population if they were able to withstand winter conditions. Some were found there in 1939 and many in 1942, and were present at all later inspections. This could be due to continual introduction of these pests with each consignment of grain, to re-infestation by the residual population, or a combination of both. It is most likely that insects had been breeding in the cavities continuously and that insecticidal treatments, while reducing numbers on the grain and in exposed conditions, did not eliminate the deep-seated residual infestations. There was a supply of food in many parts capable of supporting insects for a long period, and any treatment of goods stored in these conditions could only be palliative.

The lining boards of the walls were in a fairly good condition, although attacked by wood-boring insects, and the amount of grain found behind them is interesting. The boards ran vertically and were joined by tongue-and-groove fittings. At the top, and often below, they were covered by a horizontal bar. The bulk of the grain could not have entered from above or below and so must have penetrated through occasional faults in the boards. The first board removed in a preliminary visit to the granary revealed a mound of grain within the wall cavity about 18″ high (Pl. XIV, fig. 2), and it is difficult to explain how such a quantity might have got there. Large amounts of grain did penetrate behind the wall boards and so, presumably, there was also free access for insects.

H. pseudospretella was reported early in the records of the granary but later only infrequently, yet, when this survey was carried out, exceedingly large populations were found in the north wall cavities. It is possible that the *H. pseudospretella* had just reached such large numbers when the survey was undertaken, and that it had not been present as an appreciable component of the population beforehand. Or it could be that, unlike most of the other species which were found also upon the commodities, *H. pseudospretella* tended to remain within the cavities. The life-cycle of *H. pseudospretella* is long and adults are only found during the summer months and it may have been overlooked by inspectors.

Although the history of any sampling area could not be followed it has been suggested that by comparing insects found in areas with different amounts and qualities of foodstuffs a succession of dominant insects can be detected. That there should be a succession as the grain is used up or reduced to small particles is only to be expected, but which of the insects having similar food habits shall dominate at any one time must depend upon many different factors. The insect must be introduced in sufficient numbers to become established; it must be capable of surviving the daily and seasonal range of physical conditions; and it must be able to compete effectively with other insects occupying the same niche.

Where whole grain occurs, pests such as *C. granaria* are likely to predominate at first, but as the grain is broken by insect attack and natural deterioration, and whole grains become scarcer, such pests are likely to diminish in importance and be replaced by insects preferring broken grain. Gradually, as the grains are reduced to detritus and floury dust, *Ptinus* spp. and *T. molitor* will be favoured and dominate the population. Finally, with further deterioration, frass and inedible materials will form the bulk of the residual material and scavengers like *A. pellio* will assume dominance, and eventually be the only insects left. The dominant species may be any whose habits are favoured at the time, but the general sequence should be followed if no new grain is added. The succession is not due to new arrivals at different times, but rather to one species being better adapted to the changed condition of the food and so increasing in importance while the former dominant dies out or drops to a low level. When grain is added gradually, the succession is likely to be complicated due to more overlapping of dominance, or the resurgence of a species. Addition of fresh supplies of food will often be accompanied by new insect arrivals. If the food is similar to that already present the type of insect will also be similar, although it may be a different species. Then, according to the biology and relative numbers of the two similar species, one may be expected to replace the other, or, if they are slow breeding and one cannot replace the other in the time available before the food has deteriorated, they may occur as co-dominants. Should the new food be very different from that already present, as may often happen in a general warehouse, then the whole succession may be drastically modified.

Another factor influencing the residual population may be the introduction with new food of a species not capable of overwintering. Should such a newly introduced species arrive in large numbers, or in some other way become dominant and replace its cold-hardy counterpart in the residual population and then be eliminated by the cold weather, the residual population will be left without either of the species which one might expect to predominate with the food in such a condition. In the granary examined, the last goods to be stored on the fourth floor were Plate maize at the north end and Canadian wheat at the south end. The maize entered heavily infested with *C. oryzae*, *Laemophloeus* spp. and *T. castaneum*, while the wheat was fairly clean. In the cavities examined on the north wall, many dead *C. oryzae*, *T. castaneum* and *Laemophloeus* spp. were found and the number of *C. granaria* alive was only 10 out of a total population of insects of 600. In the area on the south wall, 181 *C. granaria* were found, representing 62 per cent. of the population. It seems possible that the introduction of the non-overwintering species *C. oryzae* and *T. castaneum* may have caused this marked difference in the concentration of *C. granaria* at the two ends of the same floor.

Of those insects found when the food supply is greatly reduced, *A. pellio* is the most important. It is known as a detritus feeder and occupies a similar position in birds' nests where it is often found when only dirt and broken insect frass are left (Woodroffe, 1953). *S. fenestralis* is often found with *A. pellio*, possibly because of its predation on other insects and the usual lag of predator behind prey. Both these species have long-lived larvae and are found when all other insects have been eliminated due to reduction in food.

Summary.

A survey of an empty granary was undertaken to assess the size and composition of its insect fauna, and the possible importance of such insects as a source of infestation of stored goods. The most important feature of the building in this connection was the presence of boarded-up cavities in the walls.

Samples were taken at random from behind all walls, from parts of the grain-distributor system, and from certain other areas.

Many grain pests were found associated with the residues. In the wall cavities large populations had been built up, reaching in one case over 2,000 insects in the food material behind a foot length of wall (the average concentration over all cavities examined was 266 insects per foot of wall).

The largest populations were behind the north and south walls and, in general, the numbers of insects increased on descending the warehouse. The difference in size of population of the different walls and stories depended largely upon the volume and quality of the débris present in the cavities. The increase in numbers was due to increase in number of species and to increase in individuals of some species.

The dominant insect in the north wall was *Hofmannophila pseudospretella* (Stnt.), in the south wall *Calandra granaria* (L.). Relative humidity probably governed the distribution of *H. pseudospretella* and caused this change in dominance. In the east and west walls, where food material was less plentiful, dominant insects were *Ptinus* spp., *Attagenus pellio* (L.), and *Scenopinus fenestralis* (L.).

When residues were in good condition either *C. granaria* or *H. pseudospretella* predominated; as the percentage of finely divided material in the residues increased so did the percentage of *Ptinus* spp. and *Tenebrio molitor* L.; finally *A. pellio* and *S. fenestralis* became dominant as the food value of the residues decreased still further, until in the end they were the only species left.

The distributor system and the superficial areas examined supported the same type of population as those cavities in which *Ptinus* spp. and *T. molitor*, or *A. pellio* were dominant.

The history of the granary, as revealed by periodic inspections between 1938 and 1951, is given and is related to the residual insect population.

Acknowledgements.

Thanks are due to the Port of Bristol Authority and the British Electricity Authority (South Western Division) for allowing the survey to be carried out and to the Inspectorate of the Ministry of Agriculture, Fisheries and Food, Infestation Control Division, for information of the impending demolition.

This work was undertaken as part of the research programme of the Pest Infestation Laboratory, and is published by permission of the Department of Scientific and Industrial Research, and the Ministry of Agriculture, Fisheries and Food.

References.

BRUCE, N. (1936). Monographie der Europäischen Arten der Gattung *Cryptophagus* Herbst mit besonderer Berücksichtigung der Morphologie des männlichen Kopulationsorgans.—Acta zool. fenn., **20,** pp. 1–167.

CANDURA, G. S. (1932). Contributo alla conoscenza morfologica e biologica dello struggigrano (*Tenebroides mauritanicus* L.).—Boll. Lab. Zool. Portici, **27,** pp. 1–56. (Rev. appl. Ent., (A) **20,** p. 714.)

COOMBS, C. W. & WOODROFFE, G. E. (1952). Two species of *Cryptophagus* (Col. Cryptophagidae) new to Britain.—Ent. mon. Mag., **88,** pp. 259–260.

MUNRO, J. W. (1940). Report on a survey of the infestation of grain by insects. —54 pp. London, Dep. sci. industr. Res.; H.M.S.O.

WOODROFFE, G. E. (1951). A life-history study of the Brown House Moth, *Hofmannophila pseudospretella* (Staint.) (Lep., Oecophoridae).—Bull. ent. Res., **41,** pp. 529–553.

WOODROFFE, G. E. (1953). An ecological study of the insects and mites in the nests of certain birds in Britain.—Bull. ent. Res., **44,** pp. 739–772.

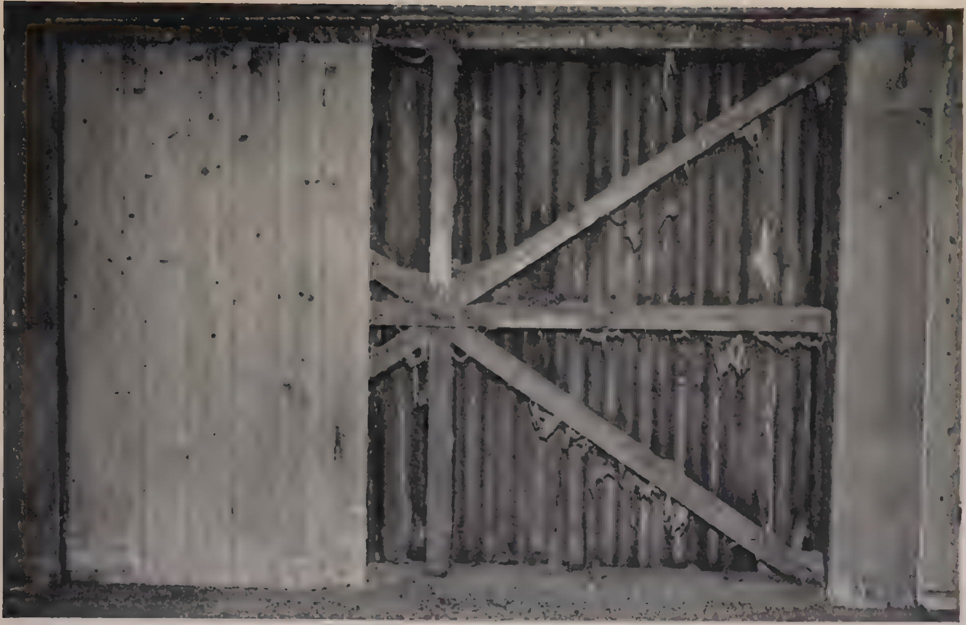


FIG. 1. A half-exposed wall-cavity compartment showing supports and débris on beams.

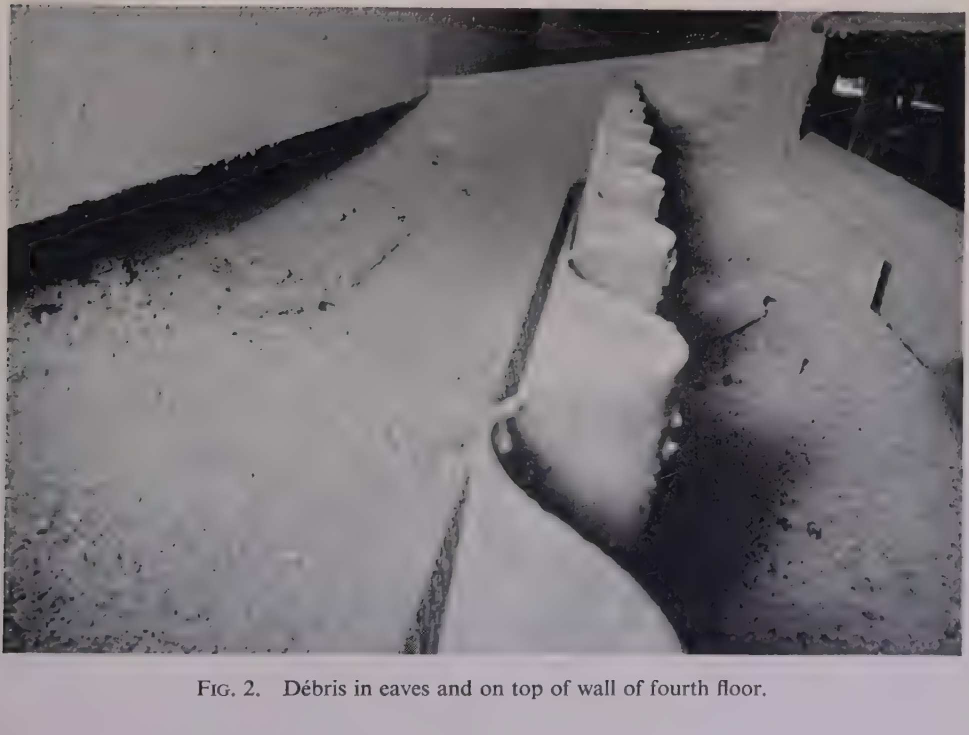


FIG. 2. Débris in eaves and on top of wall of fourth floor.

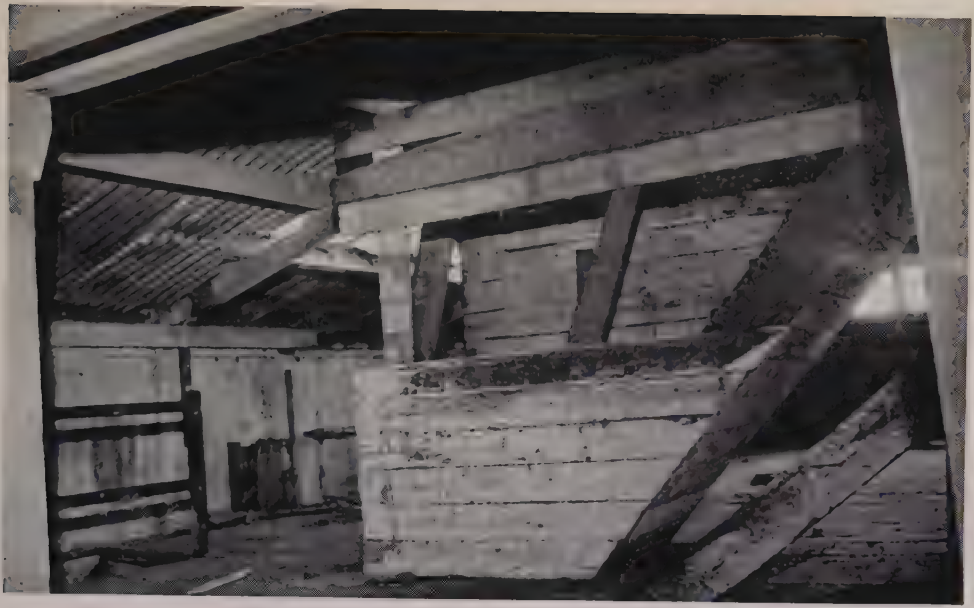


FIG. 1. Staircase on fourth floor after removal of boards for sampling.

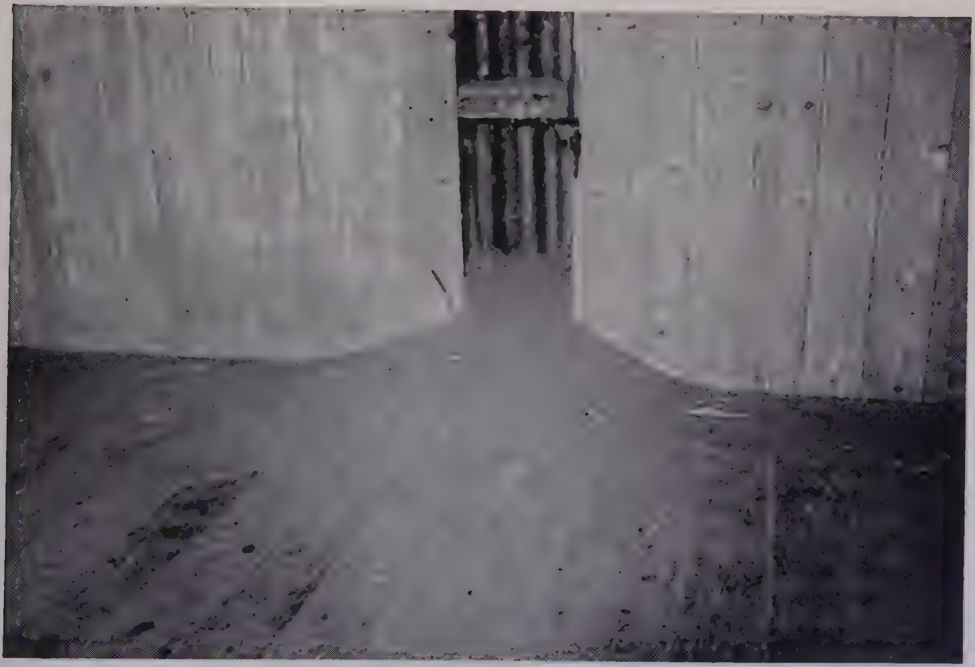


FIG. 2. An exceptionally large amount of grain found in a wall-cavity on the first floor.

THE TRANSMISSION OF BANCROFTIAL FILARIASIS ON UKARA ISLAND, TANGANYIKA.

I.—A GEOGRAPHICAL AND ECOLOGICAL DESCRIPTION OF THE ISLAND WITH AN ANNOTATED LIST OF MOSQUITOS AND OTHER ARTHROPODS OF MEDICAL IMPORTANCE.

By A. Smith, Ph.D.
Entomologist, Filariasis Reseach Unit, Mwanza, Tanganyika.

(Plate XV.)

Ukara Island lies at Latitude 1·8°S., Longitude 33·05°E. and 3,750 ft. above sea level in Lake Victoria. The island, roughly square and about 45 square miles in area, supports a population of 17,000 Africans called Bakara or Baregi. Since 1950 the health of the islanders has been studied by the East African Medical Survey and Filariasis Research Units (see Annual Reports 1950–53). As part of this programme of field survey, the writer undertook, between November 1950 and August 1953, a study of the mosquitos on the island, with special regard to the transmission of bancroftial filariasis. The present paper, which is the first of a series reporting the results of this work, contains not only an annotated list of the mosquito species on the island but also some notes on other arthropods, vertebrates (other than birds), botanical and physical features of the island and some meteorological data for the period of the observations. The agricultural practices of the people of Ukara show considerable advances over the methods in use by Africans elsewhere in East Africa. A valuable account of these practices has been given by Rounce & Thornton (1945). Since they have a direct influence on the mosquito fauna, it is considered appropriate to include, in the present paper, a brief account of the agricultural customs of the islanders together with a short description of their habits, living conditions, and tribal origins. Finally, a new map of the island, compiled during the progress of these investigations, is presented (fig. 1) and provides numerous details particularly relevant to the survey and not recorded previously on maps of the island.

The People.

The population is African except for the family of an American pastor of the East African Inland Mission who has a house and school in the district of Katende (see fig. 1). The Africans are small, but active and are composed of peoples of three different tribal origins: the Bakara from the west side of Victoria Nyanza, the Baregi from the east side of the lake and the Banyangombe or Bagwe from Sukumaland at the south end of the lake. At the end of the 19th century the Germans united the island under one chief, Matete. This chief was one of the Bakara, for his forefathers came from an area, near Bukoba on the west side of the lake, which is still called Ukara. When chief Matete was installed, the island became widely known as Ukara and the people, irrespective of their origin, as Bakara. The alternative names, Liregi for the island and Baregi for the people, are now dropping out of usage, for later chiefs have also been of Bakara stock. The original Bakara and Baregi have largely intermarried and their customs have intermingled, but village elders know and are proud of their origins. The people from Sukumaland, or Bugwe as they call it, have intermingled to a much lesser degree than the other two tribes and their customs, while largely typical of Ukara, have affinities with Sukumaland customs. These affinities are apparent in marriage ceremonies, beer-making and in the use of dried grasses as vegetables, as well as in their dialect. The Banyangombe are restricted to the south-west side of the island and the districts Bumiro, Masaka, Buyembe, Chigara and Katende are collectively called Nyangombe by the inhabitants of the island.

Geography.

The island consists of a large central area of uninhabited grassland with extensive deep erosion (Pl. XV, fig. 4), boulder ridges which rise to some 800 ft. above lake level and a coastal belt of intense cultivation. Rivers rise near the centre and, as they reach the coast, spread over wide beds to form large irrigated areas in the case of the valleys of the rivers Mukasenyi, Nyakatende, Kamugari and Musale. Sources of rivers are often situated in caves, from the roofs of which water seeps and is directed into channels. The coastline chiefly comprises long stretches of sand with boulder outcrops. The peninsulas of Chibasi and Buyombe are largely rocky and the north shore has small irregularities with scattered rocks

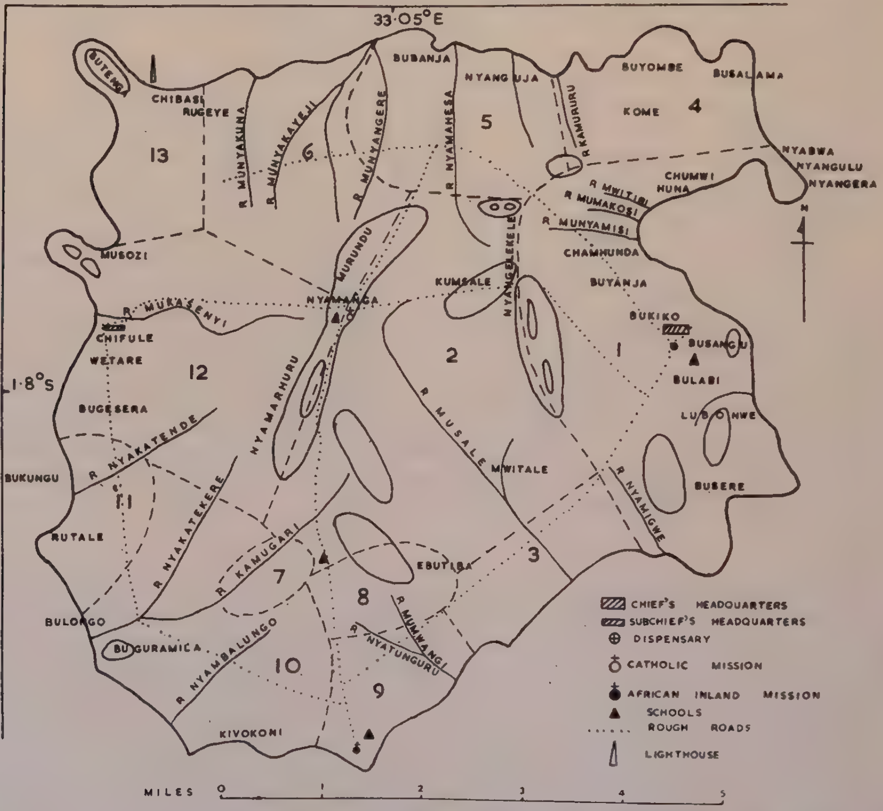

33·05°E
BUTEMBA
CHIBASI
RUGEYE
BUBANJA
NYANG UJA
BUYOMBE
BUSALAMA
KOME
4
5
13
6
R MUNYAKUNA
R MUNYAKAYEJI
R MUNYANGERE
R NYAMAHESA
R KAMURURU
NYABWA
NYANGULU
NYANGERA
CHUMWI
HUNA
R MWITIBI
R MUMAKOSI
R MUNYAMISI
CHAMHUNDA
N
MUSOZI
MURUNDU
KUMSALE
NYANGELEKELE
BUYANJA
R. MUKASENYI
NYAMANGA
BUKIKO
CHIFULE
WETARE
BUSANGU
1·8°S
12
2
1
BULABI
BUGESERA
NYAMARHURU
R MUSALE
LUBONWE
R NYAKATENDE
BUKUNGU
11
MWITALE
R NYAMIGWE
BUSERE
R NYAKATEKERE
RUTALE
R KAMUGARI
7
EBUTIBA
3
8
R MUMWANGI
BULONGO
R NYATUNGURU
BUGURAMICA
R NYAMBALUNGO
10
9
KIVOKONI
CHIEF'S HEADQUARTERS
SUBCHIEF'S HEADQUARTERS
DISPENSARY
CATHOLIC MISSION
AFRICAN INLAND MISSION
SCHOOLS
ROUGH ROADS
LIGHTHOUSE
MILES
0
1
2
3
4
5

Fig. 1.—Ukara Island. Broken lines demarcate present district boundaries, the districts being numbered on the map as follows:—
(1) Bukiko; (2) Bumiro; (3) Chigara; (4) Buyombe; (5) Bubanja;
(6) Mbule; (7) Buyembe; (8) Masaka; (9) Katende; (10) Bwisya;
(11) Bukungu; (12) Chifule; (13) Chibasi.
The rough contours are to show high areas and are the results of measurements.

and reeds, but the shores between Chifule on the west, round to Busere on the east, comprise long sweeps only infrequently interrupted by rocks. The volcanic origin of the island is shown by weathered streams of lava which radiate from the centre and by volcanic "bombs" on boulder ridges.

There are thirteen districts, each named after the principal village and each with a headman. The present chief, Mataba, resides at Bukiko village. Much of the land of Bukiko district (1) is owned by the chief. The boundaries of this district extend to the Huna peninsula in the north, the grassland and rocky peaks of Nyangelekele to the west and to Busere in the south. Several sand rivers, of which the three largest are the Mwipibi, Mumakosi and Munyamisi, and which are dry except during the rains, drain into Bukiko bay. The greater part of the Bumiro district (2) is grassland with rocky prominences and deep erosion gullies draining into the river Musale. It is bounded by Nyangelekele on the east, the Bukiko–Chibasi road to the north and the high grassy plateau of Nyamarhuru on the west. Bumiro village is very large and lies in a wooded area between the two small districts of Buyembe (7) and Masaka (8). Masaka and Katende (9) are well wooded, the trees being chiefly wattle. Two small rivers, the Mumwangi and Nyatunguru rise in Masaka. Katende is heavily populated, for it is near to Ukerewe Island, and supports fishermen as well as cultivators. Bwisya (10) is a large district with coastal irrigation from the lake at Kivokoni and whose large rivers Kamugari and Nyakatekere provide extensive irrigated areas. The river Nyambalungo is a sand river. The small district of Bukungu (11) supports a large population on crops grown in the valley of the river Nyakatende. Chifule (12) is the district with the sub-chief as headman. In addition to crops grown in the river Mukasenyi there is a small amount of irrigation from the lake. With the exception of the river Musale, which rises at Kumsale and flows to the south-east coast, the rivers on the west side of the island are longer and have a more gentle incline than those on the east side. The large rivers flowing to the west coast rise in the grassy plateau of Nyamarhuru and the rivers of the Mbule district (6) in the Murundu area. Chibasi (13) has no rivers but as it is a good district for growing red millet there is probably a rainfall heavier than average on this corner of the island. Near the bottom of Butenga peninsula, at Chibasi village, there is a lighthouse. Mbule (6) is a big drainage area with sand rivers rising in the steep Murundu hills and lies in a basin between the banked-up sandy beach and the Murundu hills. There is a vast amount of seepage from the hills and some from the lake so that a big irrigated area is available. Buyombe (4) is largely rocky and thinly populated. There is a fertile neck of land between Chumwi and Buyombe village. Until recently this district was divided into districts Kome and Huna, but "Kome" is now reserved for a small area embracing a few villages around Kome village and "Huna" is used to describe the small peninsula with villages Chumwi, Huna, Nyangulu and Nyangera.

There are several rocky islands, each a few yards wide, near the coast of Ukara. In particular there is a large group of such islands—with a rich avifauna—off Bulongo on the south-west coast (see fig. 1) and another large cluster between Rugeye and Bubanja on the north coast.

Roads, shown on the map, have been made in recent years and are footpaths enlarged to about 8 ft. wide. They are all passable to bicycles and some to motor-bicycles.

Villages and Huts.

Most villages lie concealed amongst trees in the coastal belt. The trees are pollarded to induce the growth of long shoots which are used in the construction of huts. Most huts are cone-shaped and made of wattle and thatch (see Pl. XV, fig. 1). Their average height is a little over 20 ft. and they exceed 20 ft. in diameter at the base. People and cattle are housed together, people in one half of the hut and cattle in the other. A door, 5–6 ft. high and usually less than 2 ft. wide, leads into the cattle section which is separated from the people's section by an incomplete partition of boards, grass or canes. The Bakara cook at the back of the hut and slightly inside their own section. Cattle stand on a pit filled with grass which becomes a rich compost when sufficient manure is mixed with it. A fowl perch is placed about 6 ft. above the compost pit.

Increasing population, in conjunction with increased contact of the Bakara with Africans more educated than themselves, is slowly changing their choice of hut from cone to mud-walled types. Grassland at the centre of the island which is the chief source of thatching grass, is steadily being turned over to cultivation. Thatching grass is not plentiful now, and less is needed to thatch mud-walled than cone huts. In Katende district, grass is scarce. It is interesting to note that where mud-walled huts are being built in this district they are circular with a thatch roof as with the type of hut found in Sukumaland. In Bukiko and Nyamanga, a village near the centre of the island where there is contact with educated Africans, the choice is for the rectangular mud hut. There are about five thousand huts on the island. Special buildings are: at Bukiko village, the chief's house, baraza, dispensary, dispenser's house, native authority school and teacher's house; all these buildings have cement-plastered mud-brick walls and are limewashed. At Nyamanga village is the Catholic mission, whose main buildings are the Father Superior's house, the Chapel and five schoolrooms. The mission has almost 1,000 converts and 300 schoolchildren. At Katende are the East African Inland Mission buildings which consist of two houses of the Pastor, two teachers' huts and a mud-brick school for forty pupils. Bwisya has the only shopping centre; there are fifteen small shops with corrugated iron or mud-brick walls. Provisions include soap, blankets, rope, sugar, salt, paraffin and patent medicines, chiefly eye-lotions and liniment. The " kiangazi " winds of May–July blow sand into the eyes causing inflammation; the liniment is drunk to keep out the cold.

Village drinking water is taken from the lake or from rivers.

Plantations of wattle trees cut low to the ground, in addition to rocks screened by vegetation, are usual sites for latrines.

Climate.

Monthly rainfall figures (inches) from Ukara Island for three years are given in Table I. The average for the three years on Ukara is 62 in. compared with 39 in. at Nansio near the southern shore and centre of Ukerewe Island and 44 in. at Mwanza fifty miles south of Ukara and lying on the southern shore of Lake Victoria. In the three areas, the heaviest and longest rains occur between March and May and the short rains in November and December.

Temperatures are fairly equable throughout the year but temperatures as low as 64°F. are sometimes recorded at night in July and August and, at the other

TABLE I.

Rainfall figures (inches) for Ukara Island.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1950	4·95	3·00	6·30	1·56	3·50	0·95	6·49	5·60	1·14	11·14	3·10	2·40	50·13
1951	0·20	5·16	3·10	16·13	5·05	1·55	1·20	2·30	2·15	2·05	10·87	27·66	77·42
1952	1·74	4·95	11·36	17·61	12·34	0·10	1·00	0·98	4·72	2·92	1·64	0·10	59·46

extreme, 95°F. was once recorded one afternoon in December. Wet and dry bulb, and maximum and minimum thermometers hung under the eaves of a field laboratory showed that the mean maxima were 81°F. for April, 83°F. for May, 82°F. for June and 81°F. for July 1953. The mean minima were 70°F. for April, 68°F. for May, 69°F. for June and 67°F. for July. Noon readings from wet and dry bulb thermometers showed December to be the hottest and driest month in 1952 with a temperature of 86°F. and relative humidity of 40 per cent. at midday. April was the most humid month, the temperature being 76°F. and the relative humidity 74 per cent. The lowest noon temperatures were recorded in May, the average being 73°F. with a relative humidity of 73 per cent.

A sensitive anemometer, mounted on a 6 ft. pole, supplied measurements of wind velocity. The average noon wind velocities, in metres per second, from records kept for six months in 1952–3 were: June, 4·8; July, 2·9; September, 3·0; October, 2·8; December, 2·7; and January, 2·4. Winds from the north blow from November to April. Strong winds from the east in May herald the long dry season. The winds from the east bring coughs and colds to the inhabitants but they are particularly dangerous in July and August, for serious fires break out and sweep from hut to hut in the path of the wind.

Lake Level.

Seasonal rise and fall in lake level (Table II) has little effect in general on the lacustrine contour of the island or on the cropping practices. The latter are more affected by seasonal variations in rain actually falling on the island, but in a few localities, where irrigation is aided by seepage from the lake, the rise in lake level which occurs about April or May gives wider irrigation. These areas are dealt with below. In other areas the rise in lake level which follows the rains is harmful to crops. On beaches where sand cannot be banked up, as near the bay at Bubanja, strong winds or a slight rise in lake level may flood some land too deeply to support crops. A more lasting effect on the island's lacustrine contour and agriculture is the recent annual rise in lake level (Table II). Some areas, such as at Bubanja, that were cultivated a few years ago are now submerged, but the inhabitants have compensated this emargination by extending irrigation further inland. In consequence of a new agreed lake level in connection with the Jinja dam and Nile water conservation it is likely that the considerable increase in lake level which occurred in 1952 will be permanent.

TABLE II.

Lake level readings 1950–52.

	No. of cm. above or below zero observed at Kisumu												
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mon. Av.
1950	−56	−3	−4	+18	+11	+8	+4	−4	−9	−12	−8	−20	−6·6
1951	−28	−25	−27	−3	+16	+17	−51	−15	+91	+91	−17	+17	+5·5
1952	+40	+40	+46	+62	+75	+84	+80	+65	+57	+6	+49	+50	+54·5

The zero line is 11m. 11cm. at Kisumu.

Soil.

The results of analysis of a composite top soil of six samples and a single profile dug in grassland at the centre of the island are given in Table III. It was found difficult to extend the profile below four feet when a compact but friable murram was reached. The same difficulty was experienced in further diggings so that it appears that in some areas at the centre of the island there is a high murram table and this, combined with a soil of reasonable permeability, gives a rapid run-off of rain-water. Ponding is rarely seen and the Government Agricultural Chemist writes of the soil: " a pale, slightly orange brown silty sand with a loosely cohering crumb structure, is particularly liable to erosion when there is loss of natural vegetative cover ". Erosion at the centre is widespread and jagged trench-like gullies, up to 25 ft. deep, act as drains carrying silt into the rivers near their sources. The Table also shows that the soil is acid, poor in organic matter and calcium, and moderately poor in phosphorus.

TABLE III.

Analysis of a soil profile taken in grassland at the centre of the island.

	Conductivity	pH	Org. C% (× 1·7 = org. matter)	Phos. p.p.m.	Calcium m.e.*%
Composite top soil	18	6·1	0·64	3·3	0·39
0–1 ft.	24	5·6	0·52	2·9	0·39
1–2 ft.	35	5·3	0·21	3·4	0·25
2–3 ft.	40	5·3	0·21	6·1	0·29
3–4 ft.	35	5·4	0·12	1·9	0·49

* m.e. = milligrammes equivalent.

Agriculture.

Bulrush millet (*Pennisetum*) and cassava, with smaller areas of sweet potatoes and bambarra groundnuts, are grown on high land and valley slopes throughout the year. The Bakara widely use tie-ridging, pitting and terracing to conserve soil and water on the valley slopes, and the island is able to support a population of 17,000 within its 45 sq. miles, because advanced systems of agriculture, by African standards, produce high yields of crops.

Sweet potatoes, sorghum and bulrush millet, the last usually being mixed with bambarra groundnuts, are grown in irrigated areas between October and April. The largest irrigated areas are the valleys of rivers Mukasenyi, Nyakatende, Nyakatekere, Kamugari and Musale at Chigara (see Pl. XV, fig. 2) and a wide area in the Mbule district supplied by seepage between hills and the lake. Little irrigation is possible near the source of rivers during the long rains for the beds lie in deep and narrow gullies. As the flow widens towards the river mouth it is controlled by banking up the sides of the river and directing water into channels which form a lattice across the river valley. These channels are broken at intervals to flood individual fields. Seepage water from high land at the sides of the valleys is canalised to fields and excess water diverted into channels which flow into the river. When food crops are grown between October and April there is no flooding and most channels from rivers are sealed. In fields which remain sodden sweet potatoes and other crops are planted on mounds of earth to prevent the plants rotting.

Although irrigation is largely by water derived from rainfall, there is some irrigation from the lake at Chigara, Bwisya, Bubanja, Nyanguja, and Buyanja where the general level of the ground in the coastal strip has been lowered by the removal of soil almost to lake level so that it is kept moist by seepage of water from the lake. A small fraction of the irrigated land is composed of small plots on beaches connected by channels to the lake. Channels from the lake are short, to reduce emargination and the free passage of silt from land to lake. A prominent exception is the delta of the river Musale at Chigara where there are long channels. Emargination is more than counterbalanced here by deposition of silt from the river. Rice is grown in nurseries in January and February and in March the Bakara begin to plant out the seedlings. The irrigated areas just described are almost entirely turned over to cultivation of rice, the cash crop, between April and September, if the preceding millet crop has been good. The rice ripens between July and September when it is gathered and the ground prepared for food crops. From the standpoint of varieties, although not of irrigation techniques, Ukara is in a primitive state of rice cultivation, compared with the mainland, for several varieties of inferior rice are grown mixed with the best milling variety Afaa. Several varieties of rice, with different kinds of growth-form are sown mixed together on Ukara. The chief variety, Afaa, grows erect, other varieties, Sindano, Culindi and Sena, grow semi-erect and Mburu-Mburu is a weed rice which sprawls over the ground in a rosette-shaped pattern. The presence of these inferior varieties of rice may provide advantageous breeding conditions for *Anopheles funestus* Giles compared with rice-fields on the mainland, sown almost entirely with varieties such as Afaa or Cohogo with an erect growth-form. Afaa is now being replaced on Ukara by Cohogo which is a better variety and widely grown in Sukumaland. Ukara exported 6,962 bags comprising 530 tons of rice in 1952, a favourable year.

Harvested crops are stored in small thatched containers adjacent to huts in the villages (Pl. XV, fig. 1).

Analysis shows that the soil is naturally poor in nutrients but high yields of crops are obtained by a combination of thorough digging, mixed cropping with nitrogenous plants, leaving ground periodically fallow under nitrogenous weeds and regularly manuring the ground (Pl. XV, fig. 3). The use of nitrogenous plants by the Bakara is described in a paper by Rounce & Thornton (1945). To get enough manure for their crops the Bakara support 13,000 cattle and 8,000 goats. Each hut has its cattle and goats which are confined on a pit of grass to one side of the hut. Grazing is restricted and inadequate to give the beasts enough food. Goats, and sometimes cattle, are muzzled when they pass to and from pasture. The bulk of the grass for cattle and goats is gathered by the people and the animals are to a great extent fed inside the huts. This practice entails a lot of work. A typical day's feeding requires two trips at dawn involving four miles and repeated journeys in the evening carrying a large basketful of grass weighing almost thirty pounds. The grass that is gathered for cattle is coarse and is usually from irrigated land in the beds of large rivers and in pits dug in the sandy beaches on the west and north coasts. These pits contain water and are usually 15–20 ft. in circumference, although, as at Chibasi, they may be much larger. The grass is planted in deep erosion gullies in the centre of the island and along irrigation canals at Mbule, Chigara, Buyanja. Chigara, the most highly developed of the irrigated areas, has deep ditches which extend inland from the lake, sometimes as far as 200 yards and terminate in deep reservoirs. The grass ("mabimbiri") is planted in these reservoirs which vary from 10–20 ft. wide and have banks 2–15 ft. high.

In addition to pollards about villages, mango trees are not uncommon and a few banana plants are sometimes grown near huts or in erosion gullies. Banana cultivation, which hardly existed a few years ago, is now increasing rapidly.

There is a peculiar system of land and property ownership on Ukara. Much of family property and foodstuffs is owned by women but the land is owned by the male heads of families. A man's land is divided into plots of a few square yards and he may have anything from five to thirty plots, depending on his wealth or inheritance. The plots are rarely close together but usually within a radius of two miles of his hut; sometimes, however, they are widely scattered across the island.

Plants.

Nearly all villages are built within a few yards of boulder mounds. These rocks rise to heights of from 10 to 30 ft. and are often mixed with vegetation. In the annotated list of mosquitos given below, reference is made to outdoor-resting mosquitos. Many of these were taken from a rock-vegetation association near Bubanja village. Determinations show that these plants are nearly all common East African species. *Alchornea cordifolia* (Euphorbiaceae) sprawls over the rocks like a vine and is the most conspicuous plant on rocks. Near the base of rocks are found heavily pruned *Tricalysia corbisieri* (Rubiaceae), *Markhamia* sp. (Bignoniaceae), *Canthium vulgare* (Rubiaceae), and *Rauwolfia caffra* (Apocynaceae); *Leonotis nepetaefolia* (Labiatae), *Coleus* sp. (Labiatae) and *Oldenlandia herbacea* (Rubiaceae) grow close to the bottom of rocks. Trees such as *Anthocleista* sp. (Loganiaceae), *Cassia siamea* (Caesalpiniaceae) and *Bridelia micrantha* (Euphorbiaceae) grow in the vicinity.

Vertebrates.

Mammals received most study but common amphibians and reptiles were also collected. The avifauna is interesting and extensive; it has not yet been found practicable to study it.

AMPHIBIA.

Rana occipitalis, common African bullfrog. Abundant in rivers during the rains.

Bufo regularis, common African toad. Common in huts.

Hyperolius sp., tree frogs. Uncommon.

REPTILIA.

Varanus niloticus, monitor lizard. Very common among rocks at the sides of rivers and near the lake.

Agama atricollis, agama lizard. Abundant on rocks.

Mabuia striata, Grant's skink. Common on rocks and on the walls of mud huts.

Hemidactylus brookii, gecko. Uncommon on mud-walled huts.

Chameleon dilepis, flat-necked chameleon. Common on shrubs and in trees.

Philothamnus semivariegatus, green tree snake. Occurs in shrubs, grass and roofs of huts.

Naja nigricollis, black-necked cobra. Single juvenile specimen taken in field of cassava.

Lycophidion capensis, Cape wolf snake. Single specimen taken in grass.

Python sebae, African python. Common near rivers and lake.

Pelusios sinuatus, Natal terrapin. Common in swamps.

Crocodilus niloticus, African crocodile. Common on rocks at edge of island.

MAMMALIA.

Atelerix pruneri, African hedgehog. Common in fields and under shrubs. Nocturnal.

Epomophorus wahlbergi, epauletted fruit-bat. Not uncommon in mango trees.

Taphozous mauritianus, tomb bat. Uncommon. Rests on the bark of trees.

Lavia frons, yellow-winged bat. Common in mango trees and bushes amongst rocks.

Nycteris hispida, small-eared hollow-faced bat. Not uncommon. Inhabits dark dry caves, pollarded trees, mud-walled huts (" bandas ") and under the eaves of grain stores (see Pl. XV, fig. 1).

Graphiurus murinus ssp., forest dormouse. Single specimen taken from the wall inside a mud hut.

Rattus rattus, black rat. Black and grey phase. Abundant in storehouse at Bwisya. Occasional specimens in buildings near the centre of the island.

Rattus coucha ssp., multimammate rat. Abundant in fields, not uncommon in huts.

Atilax paludinosus mordax, marsh mongoose. Scarce, nocturnal.

Genetta tigrina ssp., bush genet. Uncommon. Crepuscular. Lives among rocks at Busangu.

Heterohyrax syriacus diesneri, rock-rabbit or hyrax. Very common amongst rocks near most villages. Their breeding season is May–July when their plant food is abundant. Under natural conditions they feed on the leaves and shoots of *Alchornia cordifolia*. During these months they are retiring and inconspicuous for vegetation screens their rocky haunts. When vegetation becomes sparse in September–December they are commonly seen basking on rocks.

Invertebrates.

CULICIDAE.

The mosquito fauna might be expected to be of interest because of the geographical situation of the island as well as the influence on it of the agricultural activities of the Bakara. Isolation is probably not very important as there is a linkage to the mainland through two islands. Sizu Island is five miles south of Ukara and lies between Ukara and Ukerewe Island. Sizu is about two and a half miles long by one mile wide. Ukerewe Island is separated from the mainland only by a narrow channel. An important feature is the heavy rainfall of Ukara which has 60 inches per annum compared with about 40 inches in Ukerewe Island and at Mwanza on the southern shore of the lake.

Terms used by Haddow & others (1951) are employed here to express relative abundance of different species. In order of magnitude the terms are " abundant ", " very common ", " common ", " not common ", " uncommon ", " scarce ", " rare ", and " very rare ".

Anopheles coustani Lav.

Biting.—When human bait is available indoors and outdoors, the bait outdoors is more heavily bitten. Bites at night. Collections include the type form and var. *ziemanni* Grünb. (see below).

Resting.—Inside huts and on vegetation sheltered by rocks.

Breeding.—In rice-fields, swamps and weedy pools in deep, shady erosion gullies. Larvae not separated from var. *ziemanni*.

Abundance.—Common in a village (Bubanja) near a swamp shortly after the long rains. Scarce in the same village at other times of the year. Scarce at all times in a village (Nyamanga) away from a swamp.

A. coustani var. *ziemanni* Grünb.

Biting.—Caught off human bait.

Resting.—Two specimens taken from crevices in rocks.

A. gambiae Giles.

Biting.—When human bait is available indoors and outdoors, the bait indoors is more heavily bitten. Although it bites chiefly at night at its peak of incidence small numbers can be taken biting human bait in huts during day-time.

Resting.—Blood-fed individuals are almost entirely taken at rest in huts but unfed ones occur in caves and on vegetation. In May, *A. gambiae* forms 99 per cent. of the mosquito population resting in huts and spray catches average 287 per hut. In July, *A. gambiae* forms 75 per cent. of the mosquito population resting in huts and spray catches average 21 per hut.

Breeding.—Rice-fields are its largest source. Breeding also occurs in swamps, *Pistia* beds, grass pits, erosion gullies planted with grass, and sunlit pools in beaches and rocks.

Abundance.—Ubiquitous, reaches peak incidence in May, at the end of the long rains. At this time *A. gambiae* is abundant and can be taken off human bait at the rate of 200 per night. It is uncommon in some and scarce in other villages at the end of the long dry season.

Hosts.—Of 217 blood-fed specimens collected in huts, 199 (92 per cent.) were positive for man, 12 (6 per cent.) positive for ox and none for goat and dog. Of 17 blood-fed individuals taken from artificial pits outdoors, 14 had fed on man and two on ox.

Variation.—Many fourth-stage larvae have bifid or branched outer clypeals. Occasional specimens have single outer clypeal hairs.

A. funestus Giles.

Biting.—When human bait is available indoors and outdoors, the bait indoors is more heavily bitten. Although it bites chiefly at night it is not uncommonly found biting man indoors during the day-time.

Resting.—Blood-fed individuals are almost entirely taken at rest in huts but unfed ones occur in caves and on vegetation. In May, *A. funestus* forms 0·6 per cent. of the mosquito population resting in huts and spray catches average 1·8 per hut. In July, *A. funestus* forms 23·6 per cent. of the mosquito population resting in huts and spray catches average 6·3 per hut.

Breeding.—Rice-fields, swamps, grass pits, river beds and erosion gullies planted with grass.

Abundance.—Very common at peak incidence in July or August when it can be taken off human bait indoors at the rate of 50 per night. At the end of the dry season it is uncommon in some and very rare in other villages.

Hosts.—Of 96 blood-fed specimens collected in huts, 77 (80 per cent.) were positive for man and none for ox, goat and dog.

A. funestus var. *confusus* Evans & Leeson.

Represented by three larvae collected, respectively, from a seepage in an erosion gully, a rice-field and the grassy bed of a river.

A. longipalpis (Theo.).

Biting.—Caught off cow and goat in a hut.

Resting.—Almost entirely outdoors. Common in artificial pits in the ground near a village (Nyamanga).

Breeding.—Unknown.

Abundance.—Common in artificial pits in July. Rare at other times.

Hosts.—Of seven specimens from huts, three were positive for man and two for ox. Thirty-one blood-fed specimens resting in an artificial pit were examined for blood of man, ox, sheep or goat, dog, fowl, rat and hyrax. One was positive for man, one for dog and two had multiple feeds on man and dog.

A. maculipalpis Giles.

Biting.—One specimen was taken off human bait seated outside a hut in June at night.

Resting.—One specimen was collected in a hut in July and a few specimens taken in July from an artificial pit.

Breeding.—An adult emerged from a pupa taken in a grassy seepage in June.

Hosts.—A single specimen taken resting in a hut had fed on ox.

A. pharoensis Theo.

Biting.—Bites man mainly indoors and at night.

Resting.—Rests mainly in huts. A few specimens have been taken off sweet potato plants near a swamp.

Breeding.—In swamps.

Abundance.—Rare at most times. At the end of a long dry spell a sudden increase occurred in December and January followed by almost complete disappearance. This effect is noted by other authors (Haddow & others, 1951).

Hosts.—Of 33 blood-fed specimens taken resting in huts, 16 (48 per cent.) were positive for man and 7 (21 per cent.) for ox.

A. rhodesiensis Theo.

Biting.—Not taken biting man.

Resting.—Outdoors. Taken resting in caves and artificial pits along a river bank. Also rests on vegetation near rocks.

Breeding.—In rice-fields, swamps, grassy pools and edges of rivers.

Abundance.—Common in June.

Hosts.—Of 55 blood-fed specimens taken from a dark dry cave, infested with bats and hyrax, and near huts, all were positive for hyrax and none for man, ox, goat, dog, bat, rat or fowl.

A. rivulorum Leeson.

Breeding.—Larvae are commonly found among *Pistia* beds in swamps.

Resting.—Outdoors; egg batches from 27 adult females of the *funestus* group found resting in huts near a swamp were all of the type species.

Variations.—Specimens referable to the form known as var. *garnhamellus* Evans & Leeson were found also.

A. rufipes (Gough).

Biting.—A few specimens have been caught off human bait indoors and outdoors at night.

Resting.—Chiefly outdoors. Not uncommonly found resting in an artificial pit in July. One specimen was taken from the side of an erosion gully and two adults resting in huts.

Breeding.—In grassy pools and edges of rivers.

Abundance.—Uncommon—scarce.

Hosts.—Of two specimens taken resting in a hut, one had fed on man and the other on ox. Of four specimens from an artificial pit outdoors, tested for man and ox, all had fed on ox. Of 16 blood-fed specimens tested for man, ox, sheep or goat, dog, fowl, rat and hyrax, one was positive for man, the others negative.

A. squamosus Theo.

Biting.—A few specimens taken off human bait seated outdoors at night.

Resting.—No specimens found.

Breeding.—Amongst *Pistia* in swamps.

Abundance.—Scarce.

A. wellcomei Theo.

A single specimen taken off human bait seated outdoors, near a swamp, in June.

Uranotaenia balfouri Theo.

Larvae found in a water-hole with grass, in a grass pit and in grassy seepages.

U. alboabdominalis Theo.

A single larva taken from a water-hole with grass in December.

Aëdomyia africana Nev.-Lem.

Resting.—A single adult female was found resting in a cave in November.

Breeding.—Larvae common among reeds and *Pistia* beds in coastal bays.

A. furfurea (End.).

A few adults of both sexes taken on the leaves of sweet potato and other vegetation near a swamp.

Ficalbia (*Mimomyia*) *splendens* (Theo.).

Larvae common among *Pistia* and reeds in coastal bays and also in grassy pools.

F. (*M.*) *uniformis* (Theo.).

Larvae collected from a ground pool, a water-hole with thick grass and in *Pistia* beds.

F. (*M.*) *lacustris* Edw.

A few larvae found in coastal swamps with *Pistia*, reeds and floating grass.

Taeniorhynchus (*Coquillettidia*) *metallicus* (Theo.).

Represented by three adult males. One taken resting in an erosion gully in November and two off bushes near huts in March.

T. (*Mansonioides*) *africanus* (Theo.).

Biting.—When human bait is available indoors and outdoors the bait outdoors is much more heavily bitten. Although it bites chiefly at night it will bite a man in the shade quite readily during the day-time.

Resting.—Principally outdoors. Can be found in large numbers in crevices in rocks and on grass, pollarded bushes, sweet potato leaves and low-lying vegetation. Shows a slightly stronger preference for resting in dark places such as crevices in rocks, than *T. uniformis*. Small numbers of blood-fed specimens can be taken resting in huts.

Breeding.—In *Pistia* beds among swamps, in floating grass in swamps and in grass pits.

Abundance.—Very common near breeding places. Occurs in fairly regular numbers throughout the year. Scarce in villages away from breeding places.

Hosts.—Of 52 blood-fed specimens taken resting in huts, 14 (27 per cent.) had fed on man and 25 (48 per cent.) on ox. Of 22 blood-fed specimens taken from vegetation and crevices in rocks, three were positive for man, four for ox, two for fowl, one for hyrax and none for goat, dog, rat and bat.

Variations.—The dark scales in different individual mosquitos vary from ebony black to dark buff.

T. (*M.*) *uniformis* (Theo.).

Biting and resting habits.—Similar to *T. africanus.*

Breeding.—Occupies habitats similar to those of *T. africanus.*

Abundance.—Very common near breeding places. There is an indication that whereas *T. uniformis* is more numerous during wet months, *T. africanus* is more numerous during dry months.

Hosts.—Of 36 blood-fed specimens taken resting in huts, 10 (26 per cent.) had fed on man and 22 (61 per cent.) on ox. Of 25 blood-fed specimens taken from vegetation and crevices in rocks, one had fed on man, seven on ox, two on goat and one on dog.

Variations.—Dark scales vary from dark buff to ochreous.

Aëdes (*Mucidus*) *scatophagoides* (Theo.).

A single female collected off human bait outdoors in May.

A. (*Stegomyia*) *aegypti* (L.).

Biting.—Principally a day-time biter outdoors in the shade of trees and bushes.

Breeding.—In a rot-hole in the trunk of a mango tree, and in rot-holes in pollarded trees. No breeding in domestic utensils has been observed.

Abundance.—Uncommon during the rains. None observed at the end of the dry season.

A. (*S.*) *apicoargenteus* (Theo.).

Biting.—A day-time biter outdoors in the shade of bushes. There is a peak after dawn and another before sunset. Biting appears to be almost completely inhibited by darkness.

Resting.—Amongst foliage of bushes from which hungry females fly out to bite human bait nearby.

Breeding.—In rot-hole in mango tree and in pollarded trees. It appears possible for breeding to continue very locally during the long dry season (June–October). A pool in the divided trunk of a mango tree persisted throughout the dry season and contained larvae and pupae of *A. apicoargenteus* and *A. africanus.* A deep and loose layer of sticks and leaves lay over the pool and no doubt delayed evaporation.

Abundance.—Not uncommon during the rains and short dry season (January and February). Very rare towards the end of the long dry season.

Variations.—A few pale scales on the scutellar lobes of some specimens. There are also two types of hind-tarsal markings: in some specimens the fifth segment is all black and in others white at the base.

A. (*S.*) *africanus* (Theo.).

Biting.—Following a peak after dawn, biting-activity is maintained at a low level throughout the day-time until just before dusk when the incidence rises to a peak which is spread over to an hour after dusk. There is a very low level of biting throughout the night. A few specimens have been taken biting man in huts at night.

Resting.—As for *A. apicoargenteus*, also crevices in rocks and an occasional specimen is found resting in a hut.

Breeding.—Occupies similar habitats to *A. apicoargenteus.*

Abundance.—Common during and shortly after the rains. Very rare towards the end of the long dry season.

A. (*S.*) *metallicus* (Edw.).

Adults bred out from rot-holes in trees at Katende village in the southern tip of the island. Not recorded in other parts of the island.

A. (*S.*) *vittatus* (Big.).

Biting.—Bites mainly during the day-time in shady places outdoors. Occasional specimens taken biting at night. Very rarely caught biting in huts.

Resting.—One female found resting in a hut. A few specimens collected from an artificial pit outdoors.

Breeding.—In rock pools exposed to the sun.

Abundance.—Unknown. Larvae and pupae commonly occur in rock pools during the rains but adults are scarce as measured by catches off human bait. There may be other hosts and a great loss of larvae and pupae by rain flushing out rock pools.

A. (*Aëdimorphus*) *argenteopunctatus* (Theo.).

Represented by 29 females collected from the sides of erosion gullies, one female off the bank of a river and another from a crevice in a rock.

A. (*A.*) *dalzieli* (Theo.).

An imperfect female specimen possibly of this species was taken from vegetation at the base of a rock near a swamp.

A. (*Banksinella*) *circumluteolus* (Theo.).

Represented by three adult females, two collected off sweet potato leaves and one off low-lying vegetation near a swamp.

Culex (*Lutzia*) *tigripes* Grp.

Resting.—In caves, sides of erosion gullies and vegetation.

Breeding.—Larvae not uncommonly found in rice-fields. Also breeds in grass pits.

C. (*Culex*) *poicilipes* (Theo.).

Biting.—Has not been taken biting man.

Resting.—Rests outdoors. In large numbers on low-lying vegetation near breeding places. Rests in crevices in rocks and caves and on the sides of erosion gullies.

Breeding.—In swamps, stagnant pools with algae and amongst reeds and *Pistia* plants.

Abundance.—Common, as measured by numbers resting outdoors.

Hosts.—Of ten blood-fed specimens collected from rocks and vegetation, one had fed on both man and goat, two on goat and one on fowl. All were negative for ox, dog, hyrax, rat and bat.

C. (C.) *annulioris* Theo.

Biting.—When human bait is available indoors and outdoors the bait outdoors is more heavily bitten. It is almost entirely a night biter.

Resting.—On the walls inside huts, in caves, crevices in rocks, on grass and low-lying vegetation.

Breeding.—In stagnant water often containing green algae, seepages, rice-fields and swamps.

Abundance.—Common shortly after the rains, uncommon during the dry season.

Hosts.—Blood-fed specimens from huts have fed largely on ox. Of 147 tested, 12 (9 per cent.) were positive for man and 114 (77 per cent.) for ox. They also feed on domestic fowl.

Variations.—Median pale spots on the tergites vary from small triangles to wide bands. The wide-banded condition is the most common.

C. (C.) *annulioris* ssp. *consimilis* Newst.

Two adult females, one from an artificial pit in March and another off vegetation in June.

C. (C.) *argenteopunctatus* ssp. *kingi* (Theo.).

A single adult female taken resting in an erosion gully.

C. (C.) *univittatus* Theo.

Biting.—When human bait is available indoors and outdoors the bait outdoors is more heavily bitten. It is mainly a night biter but small numbers do bite man in shade outdoors during the day-time.

Resting.—Mainly outdoors, in crevices in rocks, caves, on low-lying vegetation, sides of erosion gullies and pollarded trees.

Breeding.—At edges of grassy pools and rivers, in seepages and in stagnant water in rocks.

Abundance.—Abundant at most times, as measured by the population resting outdoors. Not uncommon in May and scarce during the dry season, as measured by catches off human bait.

Hosts.—Blood-fed specimens from huts had fed largely on ox. Of 52 tested, seven (14%) were positive for man and 35 (67%) for ox. Of 28 blood-fed specimens collected from crevices in rocks and vegetation near rocks, two were positive for ox, one for dog, two for hyrax and two for fowl. None had fed on man, goat, rat or bat.

C. (C.) *univittatus* var. *neavei* Theo.

A few specimens taken resting on vegetation.

C. (C.) *antennatus* (Beck.).

Biting.—Mainly outdoors at night. Bites during the day-time in shade.

Resting.—In crevices in rocks and low-lying vegetation.

Breeding.—In grassy swamps.

Abundance.—Locally not uncommon towards the end of the rains in a village (Bubanja) near a small swamp. Very scarce in a village away from the swamp.

Hosts.—Of eight blood-fed specimens collected off vegetation, one was positive for ox and the others negative for man, goat, dog, rat, hyrax, bat and fowl.

C. (*C.*) *decens* Theo.

Biting.—Not taken biting man.

Resting.—Several specimens taken resting on low-lying vegetation near a small swamp.

Breeding.—In a swamp, in a rot-hole in a mango tree with *Aëdes africanus* and *A. apicoargenteus.* Also bred out from larvae collected from a rock pool with rotten leaves.

C. (*C.*) *duttoni* Theo.

Two larvae taken from a ground pool with dead leaves in April, and one adult female resting in a hut in May.

MUSCIDAE and SYRPHIDAE.

Twice a year, just after the short and long rains, the Bakara empty the pits which contain manure in the cattle section of their huts. The manure is stacked outside the huts for a few weeks and, when it has become compact, is carried to the fields. *Musca domestica* L. and *Stomoxys calcitrans* (L.) are particularly common and are a nuisance indoors during the few weeks that the manure is stacked outdoors.

The people defaecate almost entirely amongst bushes or rocks, but there are also twenty pit-type latrines in use, built by government or mission workers. The pit latrines are usually without standing water but most are infested with maggots. Adult *Chrysomyia putoria* (Wied.), *Chrysomyia albiceps* (Wied.), and the Syrphid, *Protylocera haemorrhoa* (Gerst.), were taken from a typical pit latrine.

TABANIDAE.

Tabanids appear to be uncommon. One specimen of *Tabanus taeniola* P. de B. was caught on a man working in a field near a river in May and another of the same species resting on the mud wall of a hut. Three specimens of *Chrysops distinctipennis* Aust. were taken feeding, respectively, on man, cow and dog.

BLATTIDAE.

Leucophaea surinamensis (L.) is sometimes found in enormous numbers in huts, infesting baskets containing stores of millet, African beer or the remains of a meal.

CIMICIDAE.

Beds are usually badly infested with *Cimex hemipterus* (F.). Beds are raised 1–3 ft. from the ground and consist of canes bound together, or 3–4 loose boards supported by cross pieces. The frame rests on four legs sunk into the ground and is often covered with cow hide. Bed-bugs can be collected quickly by taking the frame of the bed outdoors and beating it over a sheet. The following numbers of third- and fourth-stage bed-bugs were collected from beds in twenty huts in Nyamanga village: 1, 13, 1, 31, 20, 4, 0, 23, 36, 0, 22, 4, 0, 0, 68, 11, 130, 7, 41, 0; in huts with no infestations the beds were new or the occupants slept on the floor. The Bakara attempt to exterminate bed-bugs by immersing the beds in water or putting them in the sunlight. In some cases, as with the hut with 130 late-stage bed-bugs at Nyamanga, the owner will not take the boards off his bed outdoors as it is taboo to do so.

SIPHONAPTERA.

People are occasionally attacked by Chigoe fleas (*Tunga*). Small buildings harbouring domestic fowl are sometimes infested with chicken fleas (*Echidnophaga*).

ANOPLURA.

Infestations with head-lice, *Pediculus humanus capitis* Deg., are not common because the Bakara frequently wash, and periodically shave, their heads: four (1·7%) were infested out of 239 people examined from widely scattered parts of the island.

ACARI.

Of 123 huts examined in different parts of the island, 23 (18%) were infested with the relapsing-fever tick, *Ornithodoros moubata* (Murr.). Relapsing fever occurs on Ukara, 1 per cent. of the dispensary entries being infected (East Africa High Commission, 1952). Cattle ticks, *Amblyomma variegatum* (F.), are occasionally seen in huts.

SCORPIONES.

Scorpions, *Uroplectes fischeri* Karsch, occur in numbers in grass and rocks about the centre of the island. Communities of women pluck grass for thatching in July and occasionally receive very painful stings.

Summary.

A description is given of Ukara Island, which lies in the Tanganyika part of Lake Victoria, with an annotated list of mosquitos and other arthropods of medical importance found there. There are also notes on local plants and vertebrates.

The inhabitants, called Bakara, live in cone-shaped grass huts over 20 ft. in height and diameter. People and cattle are housed together.

The area of the island is about 45 sq. miles. The 17,000 inhabitants, almost entirely African, support themselves by advanced agricultural practices involving the use of manure and nitrogenous plants. There is a coastal belt of intense cultivation and a large central area of uninhabited grassland with extensive deep erosion. The beds of rivers which radiate from the centre are occupied by large irrigated areas. Seasonal fluctuations in lake level have little effect in general on cropping practices which are affected more by seasonal variations in rainfall.

The average rainfall for 1950–52 was 62 inches per annum. Temperatures are equable throughout the year. Mean maxima for 1953 were 81°F. for April, 83°F. for May, 82°F. for June and 81°F. for July—mean minima were 70°F. for April, 68°F. for May, 69°F. for June and 67°F. for July. Wind velocities, recorded at noon, vary between 4·8 metres per second in June and 2·4 in January.

The soil is acid, poor in organic matter and calcium, and moderately poor in phosphorus. Chief food crops are bulrush millet (*Pennisetum*) and cassava with smaller amounts of sweet potatoes, bambarra groundnuts and sorghum. Rice is a cash crop—Ukara exported 6,962 bags comprising 530 tons of rice in 1952, a favourable year.

Collections of vertebrates include three species of Amphibia, 11 of Reptilia and 11 of Mammalia.

The mosquito fauna includes 13 species of *Anopheles* and 29 Culicines.

Of 239 people, four (1·7%) were infested with head lice, *Pediculus humanus capitis* Deg.; of 123 huts, 23 (18%) were infested with the relapsing-fever tick, *Ornithodoros moubata* (Murr.), and of 20 huts examined for bed-bugs, 15 were infested with *Cimex hemipterus* (F.).

Acknowledgements.

I am indebted to Mrs. E. C. C. van Someren at the Medical Research Laboratory, Nairobi, Mrs. M. E. Bagster Wilson at the East African Malaria Unit and Mr. P. F. Mattingly of the British Museum for mosquito identifications, and to Mr. H. Oldroyd, Dr. Ragge, Dr. China, Dr. Owen Evans and Mr. Browning of the British Museum for identifying other arthropods. Also to Mr. A. C. Brooks, Colonial Research Fellow, for all mammal identifications, Mr. J. C. Williams of the Coryndon Museum, Nairobi, Miss A. G. C. Grandisson and Dr. M. A. Smith of the British Museum for identifying reptiles and amphibians. Thanks are also due to Mr. P. J. Greenway of the East African Herbarium for plant identifications, Mr. B. Weitz of the Lister Institute of Preventive Medicine for precipitin tests on almost 2,000 mosquito blood-meals, the Government Chemist, Tanganyika, for soil tests and the Senior Marine Engineer, Kisumu, for mean monthly lake-level readings.

References.

East Africa High Commission [1952]. East African Medical Survey. Annual report 1951.—74 pp. [Mwanza, Tanganyika.]

Haddow, A. J., van Someren, E. C. C., Lumsden, W. H. R., Harper, J. O. & Gillett, J. D. (1951). The mosquitoes of Bwamba County, Uganda. VIII. Records of occurrence, behaviour and habitat.—Bull. ent. Res., **42**, pp. 207–238.

Rounce, R. N. V. & Thornton, D. (1945). Ukara Island and the agricultural practices of the Wakara.—Nairobi, Colony and Protectorate of Kenya Publication.

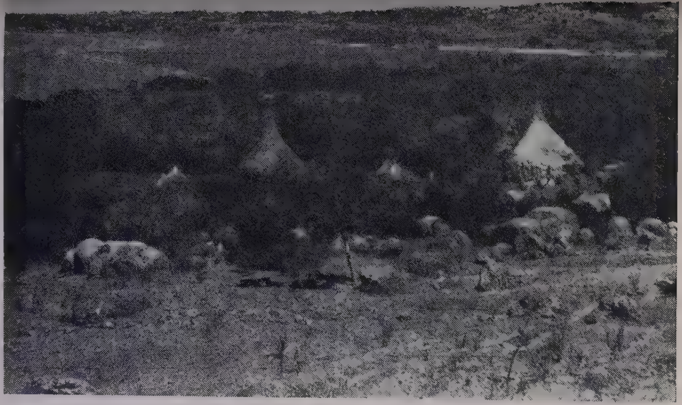


FIG. 1. Delta of River Musale showing cultivation in the river valley. The chief crop in the valley is rice.

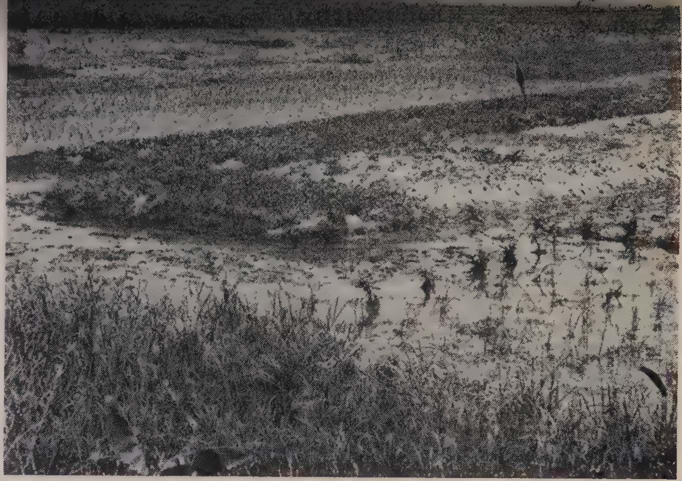


FIG. 2. Delta of River Musale showing crops grown towards the end of the year. Bulrush millet is in the background, finger millet and bambarra groundnuts in the centre and an irrigated grass which is grown as cattle fodder in foreground.

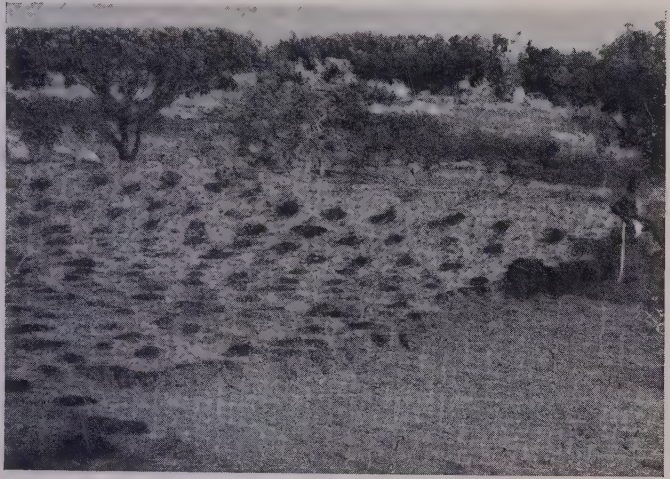


FIG. 3. Ground being prepared for bulrush millet or cassava, which are grown widely on the hill slopes. The ground is dug deeply and manured.

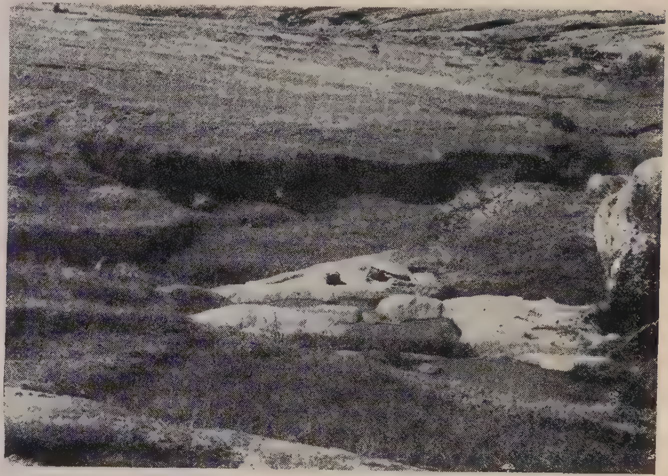


FIG. 4. River Musale near its source. Rice-fields at side of river in bottom foreground; small fields of fodder grass in the river bed.

THE TRANSMISSION OF BANCROFTIAL FILARIASIS ON UKARA ISLAND, TANGANYIKA.

II.—THE DISTRIBUTION OF BANCROFTIAL MICROFILARAEMIA COMPARED WITH THE DISTRIBUTION OF HUT-HAUNTING MOSQUITOS AND THEIR BREEDING PLACES.

By A. Smith, Ph.D.
Entomologist, Filariasis Research Unit, Mwanza, Tanganyika.

(Plate XVI.)

The transmission of bancroftial filariasis has received more study in West than in East Africa. Gordon & others (1932) and Hicks (1932), in field and laboratory studies incriminated *Anopheles gambiae* Giles and *A. funestus* Giles as principal vectors in villages of Sierra Leone. Henrard, Peel & Wanson (1946) found *A. gambiae* and *A. funestus* infected with filaria in huts in the Belgian Congo and demonstrated that full development of *Wuchereria bancrofti* took place in these species under laboratory conditions. *Anopheles* of the *gambiae-melas* type carry mature larval filariae in the Gambia (McGregor & Smith, 1952). Hicks (1932) found that complete development also occurred in laboratory infections of *A. rhodesiensis* Theo., but in view of uncertain knowledge of its feeding habits it was not possible to assess its importance as a vector. *A. squamosus* Theo. can transmit *W. bancrofti* in the laboratory, and it is found infected with a filarial worm in the field, but Hicks (1932) concluded that this species is an unimportant vector in Sierra Leone on account of its rarity. Abnormal filarial development occurred in *Aëdes aegypti* (L.) in the laboratory (Hicks, 1932) and no infections were found in wild-caught *Aë. aegypti*, but Henrard, Peel & Wanson (1946) found larvae in laboratory-infected *Aë. aegypti* to be perfectly viable and that degeneration did not occur. Immature infections of a filarial worm (thoracic forms) have been noticed in wild-caught *Anopheles pharoensis* Theo. and *A. squamosus* in Nigeria (Taylor, 1930) and in *A. pharoensis* and *Taeniorhynchus africanus* (Theo.) in the Belgian Congo (Henrard, Peel & Wanson, 1946). *Culex pipiens fatigans* Wied. is a vector in the Belgian Congo but was considered a bad vector as there was much degeneration of the worms in laboratory infections (Henrard, Peel & Wanson, 1946).

There is evidence that *A. gambiae*, *A. funestus* and *C. p. fatigans* are involved in the transmission of bancroftial filariasis in East Africa. Infective filarial forms occur naturally in *C. p. fatigans* at Dar es Salaam (Hawking, 1940) and in Zanzibar (Mansfield-Aders, 1927). *C. p. fatigans* was found to be a poor laboratory host at Mwanza (Smith, 1952). Mackay (1938) observed filarial larvae in *A. gambiae* and *A. funestus* caught at Dar es Salaam. Thomson (1951) found infections in wild-caught salt- and fresh-water *gambiae* and in *A. coustani* var. *tenebrosus* Dön. Filarial forms in the neighbourhood of the salivary glands were found in 0·4 per cent. of *A. gambiae* and 1·0 per cent. of *A. funestus* captured in huts on the southern slopes of the Usambara mountains near Tanga (Davidson & Draper, 1953).

In order to determine whether an insect is a vector of bancroftial filariasis it is not sufficient to observe developing filariae in wild mosquitos, as these worms may be of other than human origin. A good deal of other information is required including: (a) a comparison of the geographical distribution of the disease with that of different mosquito species, (b) examination of domestic and wild animals for filarial infections, (c) the sources of blood-meals of different mosquito species, (d) biting incidences on man. Gordon & others (1932) considered most of these factors and concluded that filarial infections in *A. gambiae* and *A. funestus* were of human origin in Freetown and Kissy. There have been no detailed investigations to determine vectors of bancroftial filariasis in Tanganyika and the studies on Ukara Island are intended to fill this gap. Ukara was selected for these studies because inhabitants of the island are a closely-knit and stable community. Since in Ukara it was apparent that filarial infections were not confined to *W. bancrofti* infections of man, it was necessary to undertake entomological studies of the kind referred to above in order to determine vector species of the human infection. The present paper considers the circumstantial evidence available from a comparison of the distribution of bancroftial infections of man on the island and of hut-haunting species of mosquito. Subsequent papers will deal with biting frequencies and host preferences of different mosquito species, and evidence from dissections for developmental forms of filarial worms.

The studies extended from 1951 to 1953 and were conducted from a field laboratory built near the centre of the island from which all sides could be quickly reached on foot. Staff consisted of the writer and four Africans. Nearly all mosquito identifications are by the writer and the remainder by a trained African assistant. A geographical and ecological description of Ukara is given in an earlier paper (Smith, 1955).

Filarial Infections in Man, domestic and certain wild Animals on Ukara.

Of almost six thousand night bloods, obtained from the inhabitants by medical officers of the East African Medical Survey Unit, 21 per cent. were positive for bancroftial microfilaraemia. Infections occurred in all of 26 villages studied, but were high in some villages such as Chifule (30–40 per cent.) and low in others as at Bugombe (6·6 per cent.). Except for a single infection with *Acanthocheilonema perstans* in an inhabitant who had spent several years in a *perstans*-infected area, *perstans* and *Loa loa* infections are absent on Ukara.

Filarial infections are found in many species of distantly related wild mammals in Tanganyika (Sewell, 1951). On Ukara, filarial infections occur in birds, lizard, dog and hyrax (Table I) and were detected in blood-films taken in day-time. No infections were found in cattle and goat nor in bats and multimammate rat which are the common mammals on Ukara. Monkeys and wild ungulates are absent. Wild terrestrial carnivores are represented by the scarce marsh mongoose and uncommon bush genet.

Distribution on Ukara of human Filariasis compared with Distribution of hut-haunting Mosquitos and their Breeding Places.

Densities of different species of mosquitos in huts.

The incidence of bancroftial microfilaraemia in different villages, derived from the survey mentioned above, is shown on the map (fig. 1) and in Table III.

The sampling method used for comparing the incidence of house-haunting mosquitos in different villages was to spray with pyrethrum ten huts in each village. The results for the two most abundant species, *A. gambiae* and *A. funestus*, are also given in Table III. Certain technical difficulties are imposed by the large size of the huts and their occupation by cattle and goats as well as by people. The huts (Pl. XVI, fig. 1) are cone-shaped and are over twenty feet high and twenty feet in diameter at their bases. They are built of sticks, thatched from top to bottom, but, owing to shortage of thatching grass, that on the cattle side is often thin and sometimes absent. There is a small doorway, to one side of which is a screen of grass or boards which divides a hut into rough halves, one occupied by humans and the other by cattle and goats. When spraying a hut, the procedure is to cover the floor and bed in the half occupied by humans with sheets, and to put one sheet on the floor inside the doorway which opens into the cattle half. The door is closed and pyrethrum concentrate is sprayed undiluted for ten to fifteen minutes, depending on whether the hut is small or large. Ordinary hand-operated atomisers are used and are pumped by one African assistant on each side of the screen and a third standing inside the hut by the closed door. By this means nearly all mosquitos escaping from the human half towards the door are killed by the third assistant.

TABLE I.

Microfilaraemia in domestic and wild animals on Ukara Island.

Species	Common name	No. examined	No. infected
Birds	African pied wagtail	1	1
	Black & white kingfisher	2	1
	Pigeon	6	1
	Domestic fowl	21	0
Frogs			
Rana occipitalis	African bullfrog	102	0
Lizards			
Agama atricollis	Agama lizard	65	12 (18%)
Varanus niloticus	Monitor lizard	9	0
Mammals	Cattle	110	0
	Goats	120	0
	Dogs	17	1
Atelerix pruneri	African hedgehog	16	0
Epomophorus wahlbergi	Epauletted fruit-bat	71	0
Lavia frons	Yellow-winged bat	8	0
Nycteris hispida	Small-eared hollow-faced bat	5	0
Rattus coucha	Multimammate rat	7	0
Heterohyrax syriacus diesneri	Hyrax (rock-rabbit)	28	16 (57%)
Atilax paludinosus mordax	Marsh mongoose	1	0
Genetta tigrina	Bush genet	1	0

In order to ascertain whether this method provided a representative sample of the mosquito population of the whole huts, an experiment was made in July 1952 on ten days in which mosquitos were collected in test tubes separately from the two halves of five huts. In addition to the species already mentioned in the text, the catches included *Anopheles longipalpis* (Theo.), *A. maculipalpis* Giles, *A. rufipes* (Gough), *Culex annulioris* Theo. and *C. univittatus* Theo. Each day's collection extended over fifteen minutes, and the writer and an African assistant alternated between the two halves (human and cattle) each day.

Total mosquitos from 5 huts in 10 days.

	A. gambiae		*A. funestus*		*A. longipalpis*		*A. rufipes*		*C. annulioris*		*C. univittatus*		*A. maculipalpis*	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Human half of hut	22	777	3	256	—	3	—	1	—	31	—	4	—	—
Cattle half of hut	8	357	1	90	—	5	—	1	—	8	—	2	—	1

The results show that by confining spraying to the human half of a hut one can expect a representative sample of the mosquito population resting in a hut even though the sample is not random.

Employing this sampling method, a pyrethrum concentrate was used in spraying 140 huts in May and 100 in July 1953. The total numbers of each species caught are given in Table II, from which it is clear that *A. gambiae* forms the bulk of the mosquitos resting in huts. Of 40,627 female mosquitos caught in May, 40,207 (99 per cent.) were *A. gambiae*. Of 2,793 caught in July, 2,104 (75 per cent.) were *A. gambiae*. The average number of *A. gambiae* per hut was 287 in May and 21 in July. *A. funestus* was the only other species which occurred in greater numbers than one per hut. Of the May catch of female mosquitos 247 (0·6 per cent.) were *A. funestus* and of the July catch 632 (23·6 per cent.). The average number of females of *A. funestus* was 1·8 in May and 6·3 in July. Next in abundance were *Culex* species of the *annulioris* group, with an average of 0·6 females per hut in May and 0·2 in July and *C. univittatus* with 0·3 per hut in May and 0·2 in July.

Other species represented in the collection were *A. pharoensis*, *A. longipalpis*, *C. univittatus* var. *neavei* Theo., *C. duttoni* Theo., *C. antennatus* (Beck.), *C. decens* Theo., *Taeniorhynchus africanus* (Theo.), *T. uniformis* (Theo.), and *Aëdes africanus* (Theo.).

TABLE II.

The number of mosquitos caught by spraying huts with pyrethrum in May and July 1953.

Species	May (140 huts, in 14 villages)		July (100 huts, in 10 villages)	
	♂♂	♀♀	♂♂	♀♀
A. gambiae	12,476	40,207	95	2,104
A. funestus	30	247	24	632
C. univittatus	3	44	6	20
C. univittatus var. *neavei*	0	4	0	0
C. annulioris (group) ..	9	86	0	20
T. africanus	0	6	0	10
T. uniformis	0	12	0	3
C. duttoni	0	1	0	0
A. pharoensis	0	5	0	2
C. antennatus	0	3	0	0
C. decens	0	7	0	0
Aë. africanus	0	5	0	1
A. longipalpis	0	0	0	1
Totals	12,518	40,627	125	2,793

Relationship of incidence of bancroftial microfilaraemia in villages with densities of hut-haunting A. gambiae *and* A. funestus.

The hut catches analysed by villages (Table III) indicate that villages on Ukara Island with high incidences of bancroftial microfilaraemia also have high densities of *A. gambiae* and *A. funestus*, and villages with low incidences of bancroftial microfilaraemia have low densities of *A. gambiae* and *A. funestus*. The abundance of *A. gambiae* and *A. funestus* in different parts of the island closely depends on the agricultural practices of the Bakara. Irrigated areas, shown by stippling in the map (fig. 1), are the largest sources of these two species as well as being important breeding places of *A. rhodesiensis*, *C. univittatus* and *C. annulioris*. The biggest irrigated areas are in the valleys of the rivers Mukasenyi (Pl. XVI, fig. 2), Nyakatekere (Pl. XVI, fig. 4), Nyakatende and Kamugari which flow to the west coast, the valley of the river Musale which flows to the south-east coast, and a fertile basin between shore and hills at Mbule (see maps on pp. 420 & 442). These areas are largely irrigated by water, derived from rain, which seeps from the centre of the island and high ground at the sides of the river valleys. Gravitational irrigation from the lake is found in the delta of the river Musale at Chigara, and at Mbule, Bubanja (Pl. XVI, fig. 3), Buyanja, Nyanguja and Kivokoni where it supplements irrigation by water seeping from the high land at the centre of the island.

TABLE III.

Relationship of incidence of bancroftial microfilaraemia to densities of *A. gambiae* and *A. funestus* in huts.

Village	Bancroftial microfilaraemia (%)	Total female mosquitos caught in each village			
		A. gambiae May	*A. gambiae* July	*A. funestus* May	*A. funestus* July
Chifule	30	3,622	516	25	139
Bubanja	26	7,143	162	27	38
Nyamanga	25	4,194	627	51	219
Katende	24	1,084	287	33	120
Buyanja	24	3,726	188	30	81
Busangu	24	944	—	1	—
Isiba	22	4,050	—	8	—
Bukungu	20	3,891	—	31	—
Chibasi	20	3,025	—	6	—
Huna	15	3,386	168	3	13
Bumiro	13	1,852	17	1	9
Kome	11	1,714	21	3	5
Lubonwe	9	1,277	57	1	7
Buyombe	7	294	61	1	1

The irrigated areas above mentioned are planted largely with rice between March and September and these rice-fields are the chief sources of the common hut-haunting mosquitos as well as important breeding places for *A. rhodesiensis.*

It can be seen from the map (fig. 1) that, in most cases, villages near the large irrigated areas have the highest observed incidences of bancroftial microfilaraemia on Ukara. These villages are Chifule (30%), Bukungu (20%), Bwisya (24%), Chigara (23%), Buyembe (26%), Mbule (20%), Bubanja (26%) and Katende (24%). The villages of Nyanguja (16%) and Isiba (22%) lie near rice-fields gravitationally irrigated near Nyanguja. Chamhunda (23%), Buyanja (24%) and Bukiko (23%) lie near rice-fields at Buyanja. Nyamanga (25%) lies at the head of many river valleys, far up into which there is widespread cultivation and irrigation of a coarse grass ("mabimbiri") (Pl. XVI, fig. 5), which is cut as fodder for cattle and goats. *A. gambiae* and *A. funestus* breed in beds of this grass; it is also planted in deep pits dug below the lake level in beaches (Pl. XVI, fig. 6). There are extensive grass pits near Chifule, and at Chibasi (20%) there are two lines of grass pits, some 30–40 yd. long. These pits are probably the most important source of *A. gambiae* and *A. funestus* infesting this village.

Busangu village is interesting in that 24 per cent. of its inhabitants have bancroftial microfilaraemia although there is no irrigated area nearby. There is no single large source of *Anopheles* near Busangu, but considerable numbers do infest the village when there is sufficient rain to form several kinds of breeding places. A neck of low-lying land at the base of a small peninsula between Busangu and Bulabi sometimes becomes a swamp during heavy rains. Breeding of Anophelines occurs in seepages in the sandy beach and in deep rock pools.

There are several large rock pools in Busangu village, and this is probably the only region of the island where rock pools play more than a negligible part in the production of *A. gambiae.*

Villages with low incidences of bancroftial microfilaraemia are almost invariably situated away from irrigated areas. Kome (11%) and Buyombe (7%) are situated near the sandy beach and among rocks of the large peninsula at the north-east of the island. Huna (15%) is amongst rocks but is only a mile north of the rice-fields at Buyanja. Bulabi (16%), Lubonwe (9%) and Busere (10%) are situated between sandy beaches and hills with rocks. Bumiro (13%) stands 300 ft. above the valley of the river Kamugari near its source, and Masaka (17%) is on a hill from which rise two small rivers, Mumwangi and Nyatunguru. Buguramila, although near the large irrigated area at the mouth of the Kamugari river, has a low incidence of bancroftial microfilaraemia (13%). This low incidence may have its explanation in the position of the village which stands on a hill some 300 ft. above lake level and on the east side of the river valley. Winds blow steadily from the east during the long dry season (May–October) so that villages are possibly less liable to heavy infestation of *A. gambiae* and *A. funestus* if situated to the east of the principal dry-season breeding sites of these mosquitos.

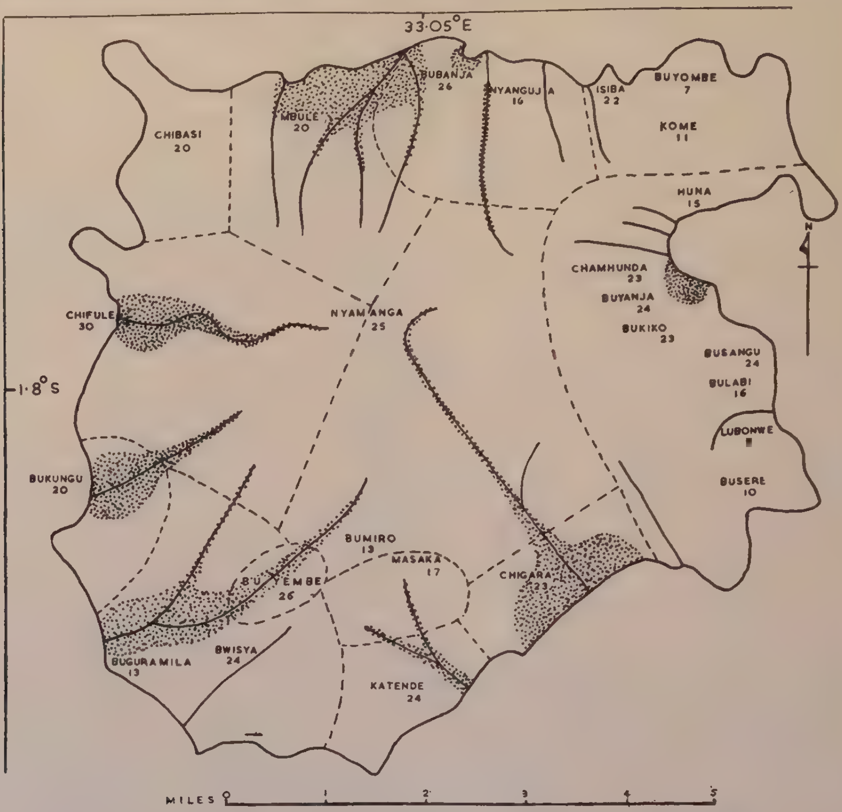

33·05°E
CHIBASI 20
MBULE 20
BUBANJA 26
NYANGUJA 16
ISIBA 22
BUYOMBE 7
KOME 11
HUNA 15
N
CHAMHUNDA 23
BUYANJA 24
BUKIKO 23
BUSANGU 24
BULABI 16
LUBONWE
BUSERE 10
CHIFULE 30
NYAMANGA 25
1·8°S
BUKUNGU 20
BUMIRO 13
MASAKA 17
BUYEMBE 26
CHIGARA 23
BWISYA 24
BUGURAMILA 13
KATENDE 24
MILES 0 1 2 3 4 5

Fig. 1.—Ukara Island, showing incidence of bancroftial microfilaraemia.

Summary.

Ukara Island was selected for studies on the transmission of bancroftial filariasis because it provided a naturally circumscribed area with a substantial human population of which adequate numbers showed microfilariae. It is a closely-knit and stable community.

Filarial infections also occur in bird, lizard, dog and hyrax (rock-rabbit) on the island. The determination of the vectors of human filariasis thus depends on evidence of different kinds, the present paper considering only the general correlation of microfilarial incidence with the distribution of common domestic mosquitos in villages of the island.

Anopheles gambiae Giles and *A. funestus* Giles form the bulk of the population of mosquitos resting in huts. There is an indication that high densities of *A. gambiae* and *A. funestus* occur in villages with high incidences of bancroftial microfilaraemia, and that most villages with high incidences of bancroftial microfilaraemia are situated near large rice-growing areas or other ecological conditions suitable to substantial breeding of these domestic mosquitos.

Acknowledgements.

Thanks are due to Mr. H. S. Leeson and Mr. S. Smith of the London School of Hygiene and Tropical Medicine for advice in preparing the maps in parts I and II of this study.

References.

Davidson, G. & Draper, C. C. (1953). Field studies of some of the basic factors concerned in the transmission of malaria.—Trans. R. Soc. trop. Med. Hyg., **47**, pp. 522–535.

Gordon, R. M., Hicks, E. P., Davey, T. H. & Watson, M. (1932). A study of the house-haunting Culicidae occurring in Freetown, Sierra Leone. . . —Ann. trop. Med. Parasit., **26**, pp. 273–345.

Hawking, F. (1940). Distribution of filariasis in Tanganyika Territory, East Africa.—Ann. trop. Med. Parasit., **34**, pp. 107–119.

Henrard, C., Peel, E. & Wanson, M. (1946). Quelques localisations de *Wuchereria bancrofti* Cobbold au Congo Belge. Cycle de développement chez *Culex fatigans* Wied., *Anopheles funestus* Giles, *Aedes aegypti* Linnaeus et *Anopheles gambiae* Giles.—Rec. Sci. med. Congo Belge, no. 5, pp. 212–232.

Hicks, E. P. (1932). The transmission of *Wuchereria bancrofti* in Sierra Leone. —Ann. trop. Med. Parasit., **26**, pp. 407–422.

McGregor, I. A. & Smith, D. A. (1952). A health, nutrition and parasitological survey in a rural village (Keneba) in west Kiang, Gambia.—Trans. R. Soc. trop. Med. Hyg., **46**, pp. 403–427.

Mackay, R. (1938). Second (final) report of the Malaria Unit, Dar es Salaam, for the period November 1934 to December 1936.—61 pp. Dar es Salaam, Govt. Printer.

Mansfield-Aders, W. (1927). Notes on malaria and filariasis in the Zanzibar Protectorate.—Trans. R. Soc. trop. Med. Hyg., **21**, pp. 207–214.

Sewell, P. [1951]. Filariasis in wild animals.—Rep. Filariasis Res. Unit [Mwanza], 1950, pp. 49–52.

Smith, A. [1952]. Filariasis vector report.—Rep. Filariasis Res. Unit [Mwanza], 1951, pp. 51–56.

SMITH, A. (1955). The transmission of bancroftial filariasis on Ukara Island, Tanganyika. I. A geographical and ecological description of the island with an annotated list of mosquitos and other arthropods of medical importance.—Bull. ent. Res., **46,** pp. 419–436.

TAYLOR, A. W. (1930). The domestic mosquitos of Gadau, Northern Nigeria, and their relation to malaria and filariasis.—Ann. trop. Med. Parasit., **24,** pp. 425–435.

THOMSON, R. C. Muirhead (1951). Studies on salt-water and fresh-water *Anopheles gambiae* on the East African coast.—Bull. ent. Res., **41,** pp. 487–502.

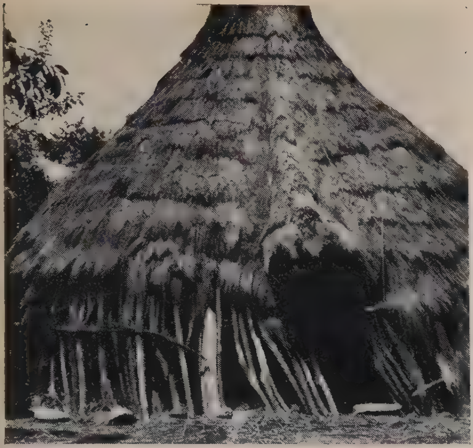


FIG. 1. A typical Ukara hut. Humans occupy the right-hand half and cows and goats the other.

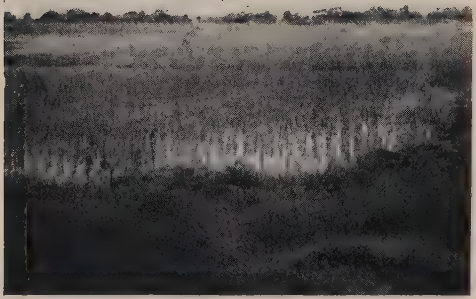


FIG. 2. Mouth of the River Mukasenyi showing extensive cultivation of rice. Rice-fields are the chief breeding places of *A. gambiae* and *A. funestus* on the island.

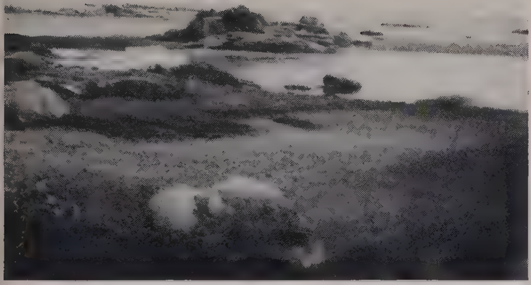


FIG. 3. Rice cultivation near the lake edge at Bubanja, kept moist by gravitational irrigation from the lake.

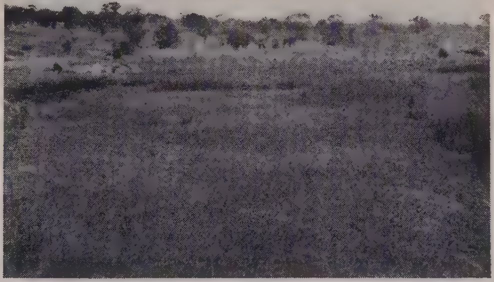


FIG. 4. Plantations of irrigated grass that provide breeding places for *A. gambiae* and *A. funestus* in bed of River Nyakatekere.

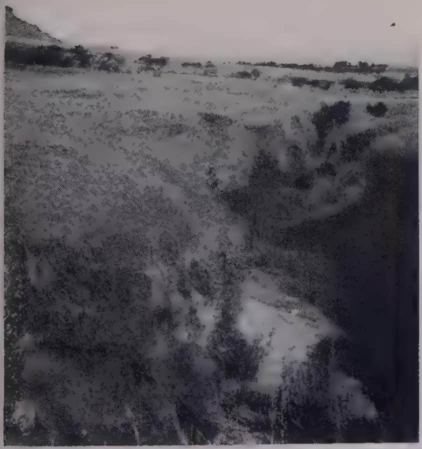


FIG. 5. An erosion gully near the centre of the island with a plantation of grass which requires irrigation and provides breeding sites for *A. gambiae* and *A. funestus*.

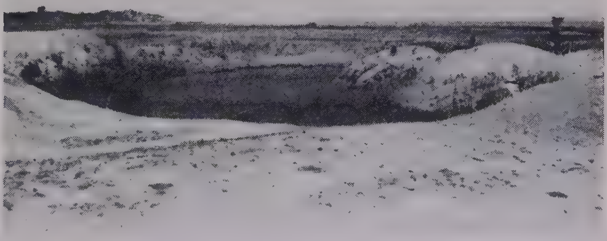


FIG. 6. A grass pit at Chigara which is a source of *A. gambiae* and *A. funestus*.

THE SPECIFIC BIOLOGICAL CHARACTERISTICS OF *ANOPHELES* (*MYZOMYIA*) *SERGENTII* (THEO.) AND THEIR CORRELATION WITH MALARIA CONTROL IN ISRAEL.

By Z. Saliternik, Ph.D.
Director, Anti-Malaria Department, Ministry of Health,
Jerusalem, Israel.

(Plates XVII & XVIII.)

Anopheles (*Myzomyia*) *sergentii* (Theo.) is of prime importance as a malaria vector in Israel at the present time and it is considered the principal autumn vector of *Plasmodium falciparum* (Kligler, 1930; Shapiro & Saliternik, 1930). It responds readily to laboratory infection. A successful inoculation rate of 53·8 per cent. (17 mosquitos) was obtained though only 0·5 per cent. of 195 mosquitos were found infected in the field (Kligler, 1930). Among 539 females collected in the north of the country, 0·2 per cent. had salivary-gland infections (Leeson & others, 1950). In Egypt, an infected salivary-gland rate as high as 2·7 per cent. of 220 females of this species was found (Mohyddin Farid, 1940). The importance of this species in maintaining malaria in Israel was further demonstrated after the great reduction of the important malaria vectors, *A. sacharovi* Favr and *A. superpictus* Grassi, following intensive residual spraying operations.

Biological data on *A. sergentii* are rather scanty in the literature. Laboratory and field observations (Saliternik, 1945) have been carried out in Israel, particularly in the Jordan, Beisan and Dead Sea valleys where it is the dominant Anopheline. These observations were made during the period 1938 to 1943, before the introduction of modern insecticides, and in the years 1946 to 1952 following their introduction and country-wide use (Saliternik, 1950, 1953).

Bionomics.

Distribution.

A. sergentii occurs from the Canary Islands and north Africa to north-west India. In Israel it is found throughout the country but reaches its greatest density in the Jordan, Beisan and Huleh valleys and various localities in the Negev.

Morphology.

Egg.—Small, rather dark and broadened, with a slight frill and many air compartments. Variations were found by the author in a small number of eggs, in which the dorsal exochorion was covered, two minute oval apertures in the extremities remaining open while the central area exhibited a long broad depression surrounded by air compartments (Pl. XVII, figs. 1 and 2).

Larva.—Clypeal hairs simple, distance between inner clypeal hairs broad; antennal shaft hair simple. Palmate hairs on all segments, occasionally absent from thorax and first segment, leaflets with apical thread-like filament. Intersegmental plates broader than alimentary tract.

The following variations in the pigmentation of the fronto-clypeus, which are possibly of genetic significance, were noted by the author in the course of many examinations:—

(a) a continuous transverse band,
(b) a shorter band with a small detached lateral spot on each side,
(c) a small transverse band, without lateral spots, which may at times be faintly divided through the middle. (Pl. XVII, figs. 4, 5 and 6.)

Adult.—Small or medium, light grey. Palpus with three white bands, apical band white, shorter than other white bands. Mesonotum with dark hairs, no scales. Wings with four white and four black alternating patches on the costal margin, the dark patches broader than the white; basal costal area dark. Light scales on all veins. Base of cubitus at bifurcation dark scaled. Length of apical band and intensity of wing scale pigmentation variable.

Hatching of eggs and emergence of adult from pupa.

Our laboratory and field observations (Saliternik, 1945) showed that a very small amount of water is enough for the maintenance of the aquatic stages. Eggs placed on water-saturated blotting paper immediately following laying, would hatch simultaneously, and the larvae would live for several days, but a surplus of water on the blotting paper is essential if the shell is to be cast off.

Larvae of all instars would remain alive on the bottom of a moist earthenware container for one to two days after all surplus water had evaporated. When water was again added, the larvae would become active and complete their development. Larvae similarly exposed in glass containers would die shortly after evaporation of the water. In the humid autumn months, larvae were frequently found alive on the moist earth bed of recently emptied irrigation canals. Similarly, numbers of third- and fourth-instar larvae would be found in the water of such canals immediately after they had been refilled.

Observations on 160 pupae placed on water-saturated blotting paper showed that in most cases the adults would emerge successfully. Should pupae happen to be stranded on moist earth in the field the adults may also emerge successfully.

Development under extreme conditions.

All aquatic stages of this species were highly resistant to changes in temperature and strength of current flow.

In laboratory conditions (Saliternik, 1945), eggs were laid and developed at a water temperature as low as 9·5°C. At 35°C., few eggs were laid and none hatched and eggs which were kept frozen for six hours died. Fourth-stage larvae subjected to a one degree rise in temperature every minute died between 41·8° and 45·5°C. In nature, a continuous water temperature of 36°C. was apparently high enough to prevent development. In the laboratory, larvae in water at 7°C. would sink to the bottom of the container, lying there for some time without dying, but in nature they were found resting in the bottom mud for considerable periods of time at 12°C. Laboratory experiments (Saliternik, 1945) showed that fourth-stage larvae would survive three days at 10°C. or frozen in ice for one hour. They would also survive a change of water temperature every 12 hours in the sequence: 24°, 7°, 25°, 6°, 23°, 5°, 23°, 5°, 26°C., demonstrating resistance to sudden and extreme temperature changes. They also show resistance to other extreme conditions; 20 per cent. of the larvae in beakers, whose water surface was covered with 5 mm. of medical paraffin for 20 hours, survived. There was a 5 per cent. survival and complete development of larvae placed in water under a film of fuel oil for $1\frac{3}{4}$ hours following which they were washed and transferred to fresh water, as in the case of the previously mentioned group. In the field, larvae cling to the banks of streams and stones, and are capable of resisting strong and sudden currents caused by the release of dammed water or by torrential rains.

Numbers of pupae have survived freezing in the laboratory for one hour, normal adults emerging.

Development rates at various temperatures.

According to our observations there is a direct and constant relationship between temperature and rate of development in the egg and pupal stages, as shown in fig. 1. Development of eggs took 13 days at a temperature of 13·0°C. and only 1½ days at 29·6°C. Development of pupae took ten days at a temperature of 11·5°C. and only one day at 30·2°C. Development in the larvae, however, is dependent on additional factors such as alkalinity, food, light, etc. The average time of larval development under laboratory conditions is six days at 28·0°C., ten at 23·8°C., 25 at 19·2°C. and 83 days at 14·5°C.

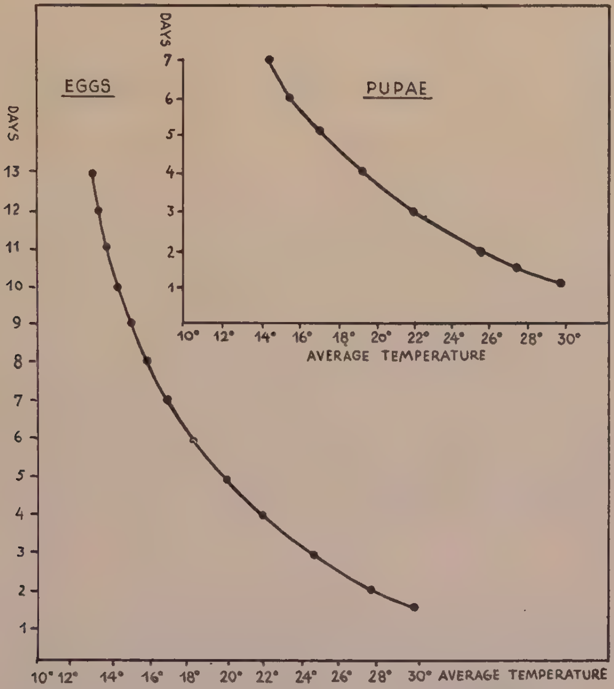


Fig. 1.—Rate of development of eggs and pupae of *Anopheles sergentii* at different temperatures.

An equation for length of time of development (Bodenheimer, 1926) is $t(T-c)=\text{Const.}$, where t = length of time in days, T = the mean temperature and c = threshold temperature for development. Graphically it is described as a hyperbola. According to this equation, the thermal constant for *A. sergentii* will be 53 and no development will occur below 8·7°C.

The quickest development of the aquatic stages occurs from May to September (Saliternik, 1945). During this period, eggs and pupae develop in 1·5 to 2 days, and on hot "khamsin" days at a temperature of 30·2°C. in as little as one day. In the hot summer days of the Beisan valley, at water temperatures as high as 30°C., the mosquito undergoes its complete cycle from egg to adult in nine days. In winter, development is rare and, when it occurs, it is slow, the complete cycle taking three months or more. The limits of temperature under which breeding was still found ranged from 12°C. to 36°C.

Characteristics of typical breeding places.

Observation on the optimal breeding sites revealed 124 places in which *A. sergentii* alone was found and 39 in which it was found in association with *A. superpictus* or *A. sacharovi* (Saliternik, 1945). The following were considered the most favourable breeding conditions:—

(1) Shallow divergencies along stream beds and shallow puddles cut off from the main stream having a depth of water usually under 15 cm.; gentle flows over gravel bottoms and shaded canals with vertical banks. Breeding was sometimes found in minute quantities of water which partly disappeared during the day.

(2) Optimal water temperature, between 23°C. and 28°C.

(3) Alkalinity, from pH 7·0 to 7·55.

(4) Because of the small volume of water frequently utilised as a breeding place and consequently the large amount of evaporation, salinity may be as high as 0·6 to 0·7 per cent.

(5) Breeding places are most frequently found where shade is provided by banks, rocks or vertical vegetation.

(6) Owing to the temporary nature of most of the breeding places of *A. sergentii*, a fixed or typical flora is lacking. Such land vegetation as *Phragmites communis* is often present. In unshaded places and in the presence of *Cladophora* or other filamentous algae, *A. sergentii* was found breeding in association with *A. superpictus*, and, if *Myriophyllum*- or *Ceratophyllum*-flora was present, with *A. sacharovi*. No breeding of *A. sergentii* was found in water which was densely covered with such aquatic plants as *Nymphea alba*, *N. caerulea*, *Lemna vulgaris*, *Lemna minor*, *Jussieua repens* and *Nuphar luteum*.

Filamentous and unicellular algae were studied from nine breeding places. Of the four filamentous algae found the commonest was *Oscillatoria*; of 18 unicellular algae, *Navicula* was the most prevalent, followed by *Synedra*.

Typical breeding places of *A. sergentii* are shown in Plate XVIII, figs. 1 and 2.

TABLE I.

Relation of number of mosquitos, expressed as percentage of annual total, to mean monthly temperature.*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean temp. (°C.) ..	12·4	13·2	15·2	18·1	21·2	24·0	26·0	26·6	25·4	23·4	18·4	14·8
Mosquitos (%) ..	0·1	0·1	0·2	0·2	1·6	1·0	5·2	2·6	28·9	32·0	17·5	10·6

* After Kligler (1930) and Shapiro & Saliternik (1930).

Influence of seasonal variations in temperature on adult density.

The relationship of the adult population of *A. sergentii* to the mean monthly temperature was shown by Kligler (1930) and by Shapiro & Saliternik (1930) and is illustrated in Table I. Considering the country-wide data, it had been assumed (Kligler, 1930) to be practically absent in the spring and summer months. Our observations in the Beisan valley in 1942, however, as shown in Table II, reveal a slight rise in adult numbers in April to June, followed by a decline and a second very high peak between September and November, the maximum generally being reached in October (Saliternik, 1945). In the autumn, *A. sergentii* is the most abundant Anopheline in the country, but from December to April the species is represented only by isolated individuals.

TABLE II.

Relation of the number of mosquitos, expressed as percentage of annual total, to monthly temperature in Beisan valley in April–December 1947.

	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean temp. (°C.)	20·3	26·0	30·6	29·7	30·0	28·7	25·2	19·2	13·0
Mosquitos (%) ..	7·0	8·0	17·0	4·0	4·0	6·0	34·0	17·0	4·0

Hibernation.

The species overwinters in all stages, larval and adult; occasional females laying eggs or with developing eggs may be found throughout the winter. At no time were females with developed fat-bodies found. Thus, in contrast to *A. sacharovi* and *A. superpictus*, no hibernation occurs in this species.

Fertility as compared with two other common important Anophelines in Israel.

Mer (1931) showed that the fertility (*i.e.*, the number of eggs laid in a single batch at different months of the year) of *A. sacharovi* is highest in April, June and August (200 to 290 eggs) and lowest in February, March and September–November; in December and January there was no oviposition.

Our observations on the fertility of three species of *Anopheles* were made near Haifa in the year 1939–40 (Saliternik, 1945). Female *Anopheles* with developed ovaries were kept individually in cages containing dishes filled with water and the eggs, which were laid on the surface of the water, were counted. After laying, the females were dissected. In the case of *A. sergentii* there were instances in which a single laying was distributed over several days. These instances are not included in the figures. The average number of eggs laid by a single female of *A. sergentii*, *A. sacharovi* and *A. superpictus* in different months of the year is shown in Table III.

TABLE III.

Fertility.

(Average number of eggs in a single batch, 1939–1940.)

Month	Av. temp. in °C.	*A. sacharovi*		*A. superpictus*		*A. sergentii*	
		No. of layings	Av. no. of eggs per batch	No. of layings	Av. no. of eggs per batch	No. of layings	Av. no. of eggs per batch
January	12·7	13*	172	3*	124	21	106
February	14·5	11*	187	2*	128	14	100
March	17·2	14	200	14	100	8	102
April	21·6	28	209	16	145	17	104
May	23·8	10	249	15	159	22	114
June	26·0	17	239	37	147	17	100
July	28·1	23	194	14	148	21	107
August	28·3	11	228	21	152	30	123
September	27·5	23	188	17	137	39	124
October	25·1	21	207	8	127	74	128
November	19·2	7	149	2	101	68	125
December	15·2	10*	152	—	—	34	102
		188	198	159	133	365	112

* Only in a warm room after several meals.

A. sergentii.—The average was 112 eggs per batch, 150 or more eggs per batch is very rare. In autumn, particularly in October, the period of most intensive breeding, the fertility rises slightly. In contrast to the other two species of *Anopheles*, oviposition continues at a reduced pace, throughout the winter.

A. sacharovi.—The yearly average was 198 eggs per batch and batches of 200 to 250 eggs were common. The peak of fertility is reached in May and June. A decline takes place during the period July to September. This is the most fertile species.

A. superpictus.—The yearly average was 133 eggs per batch with the highest fertility in spring, the peak being reached in summer. During the months of December and January, laying ceases almost completely, with observed exceptions.

In the three species studied, maximum fertility corresponds to maximum population density. It is interesting to note the differences in the fertility of the two common species, *A. superpictus* and *A. sergentii*, which are usually found together. Observations were made in two colonies in the Beisan district, in August to November 1942 (Saliternik, 1945). The average daily numbers of females of *A. sergentii* were 9 in August, 11 in September, 47 in October and 25 in November, the corresponding numbers for *A. superpictus* being 29, 18, 19 and 7, respectively. Twice weekly all mosquitos found in the stables were collected, and after determination of the species they were placed individually in cages for isolated laying. During this period, the *A. superpictus* laid 330 batches of eggs and the *A. sergentii* 500, the percentages of these figures laid monthly being shown in Table IV.

TABLE IV.

Monthly distribution of batches of eggs laid by females of *A. sergentii* and *A. superpictus* during August to November 1942.

Month	*A. sergentii*		*A. superpictus*	
	Number of batches	Percentage	Number of batches	Percentage
August ..	77	15·4	151	45·7
September ..	117	23·4	111	33·7
October ..	243	48·6	67	20·3
November ..	63	12·6	1	0·3
Total	500	100	330	100

It appears that, from the beginning of August, the number of gravid females of *A. sergentii* rises and reaches its peak during October. Meanwhile, the percentage of gravid females of *A. superpictus* drops from month to month, and, when hibernation sets in, development and oviposition cease.

Biting habits.

A. sergentii has been taken whilst biting both man and domestic animals throughout the night and occasionally in the early evening, both indoors and out-of-doors (Saliternik, 1945; Shapiro, Saliternik & Belferman, 1944). It is a particularly avid biter during the autumn and may be considered both zoophilic and anthropophilic.

Adult resting places and the use of traps for assessing mosquito density and insecticide effectiveness.

The adults of *A. sergentii* apparently prefer partly shaded corners of rooms and stables, and may be found clinging to spider webs, rafters, dark cloth or almost any vertical surfaces of material that is a non-conductor of heat. They generally attempt to hide in folds of clothing, cracks in stone walls and other such places; this, coupled with their small size and general grey colour, which often blends with the background, makes it difficult to find them.

Following DDT residual spraying operations, the adults were found, in reduced numbers, only in unsprayed places such as uncompleted buildings, cellars, caves, bunkers, etc.

In the past, the density and seasonal prevalence of various species of adult Anophelines in a given region was determined by periodic collections at appropriate outlying stations in the vicinity of a populated area. Collecting stations were generally set up in barns, stables, cellars, attics or undisturbed corners of rooms in which mosquitos naturally tend to collect in large numbers. The application of residual insecticides prevents such concentration, since the mosquitos coming in contact with sprayed surfaces are irritated and leave the collecting station or are killed during the night, before routine morning collections are made.

In such cases it is possible to study changes in mosquito populations by collecting the Anophelines during the period when they bite man or domestic animals, or by determining changes in larval populations of adjacent swamps. Both of these methods, however, are technically inconvenient and neither accurately reflects natural conditions.

In order to obviate these difficulties, traps were devised which eliminated draughts and provided twilight illumination, suitable temperatures and appropriate isolated surfaces on which the mosquitos could alight. These traps (figs. 2 & 3) were constructed of wood or cardboard, and the mosquitos collected within them in large numbers in a limited area, thus facilitating detection and trapping. The traps were set up in semi-darkness in barns and stables, in shelters and outposts, or in outdoor trenches. Some were built without bottom or without front wall, partially covered with sacking or lined with rough, dark cloth. *A. sacharovi* apparently prefers traps of the first type, while *A. sergentii* and *A.*

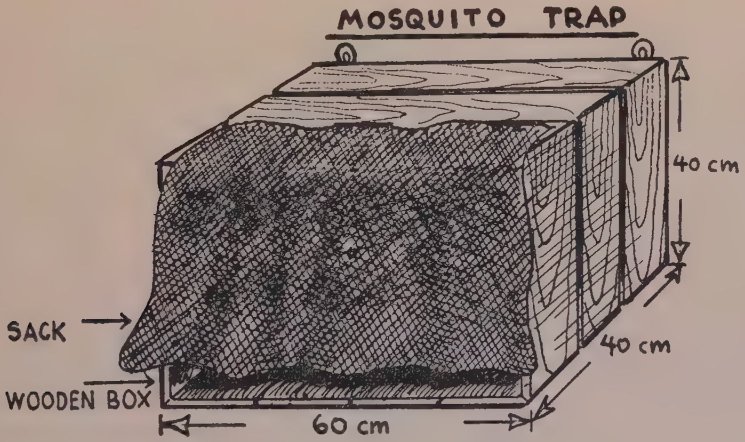


Fig. 2.—Mosquito trap, used indoors.

superpictus prefer the second. Often heavy, wool cloths were purposely hung in dark corners to serve as a point of concentration for *A. sergentii* and *A. superpictus*.

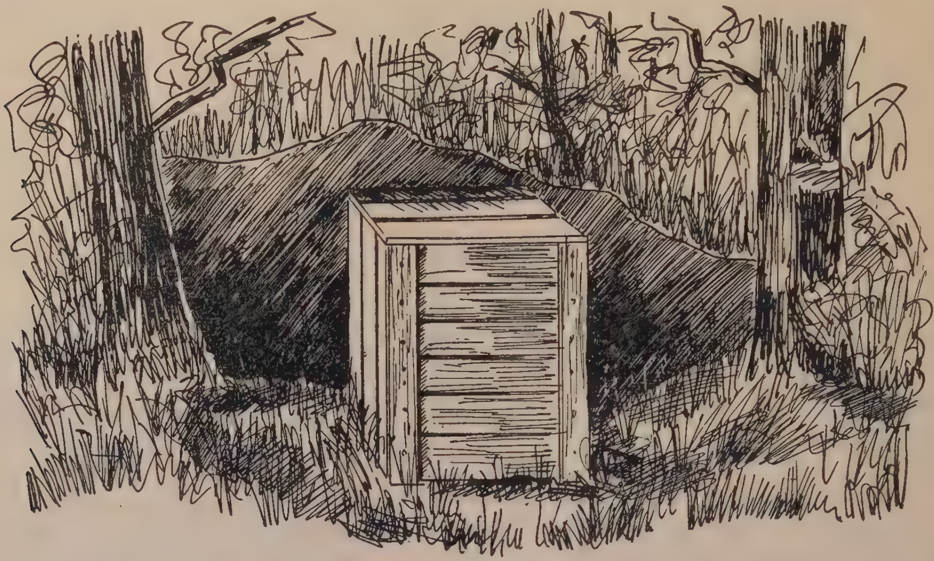


Fig. 3.—A wooden mosquito trap, used out-of-doors.

These traps were introduced before spraying with residual insecticides. Experience showed that one such trap, properly constructed and correctly placed, attracted 80 to 90 per cent. of the total number of mosquitos caught in a given room, and as many as 50 per cent. caught in several hours' collecting in an entire settlement, as is shown in Table V. In this instance the trap was of the kind illustrated in fig. 2, with the open side, two-thirds covered with sacking, facing east. It was sited in a goat shed with walls, was placed on bales of hay and reached to within half a metre of the roof. The mosquitos in a trap could be observed and caught within a few minutes. The traps were also found to be very effective in checking the presence and movement of adult Anophelines in settlements sprayed with DDT, provided that the traps themselves remained unsprayed with DDT. While not a single living mosquito was found elsewhere in

TABLE V.

Trapping of *A. sergentii* and *A. superpictus* in Maoz, Beisan valley, in September 1939.

Date of collection	Hours of collection	Number of mosquitos		
		in trap	in shed	in settlement
1.ix.39	0800	61	2	144
3.ix.39	1200	44	0	1
5.ix.39	1400	38	0	22
6.ix.39	1800	22	0	4
Total		165	2	171

a sprayed room, a few surviving mosquitos could regularly be found in the traps, their numbers varying daily with the larval density in the swamps, the local seasonal population density of adult mosquitos, and depending on whether the building had been sprayed completely or only partially and the length of time that had elapsed since the application of DDT.

Immediately after spraying, the number of mosquitos found in the traps approached zero, but their number rose as the toxicity of the residual insecticide was lost. The appearance of considerable numbers of mosquitos in the traps indicated that re-spraying was necessary, since the previous spray was no longer effective, as shown in Table VI.

TABLE VI.*

Number of Anopheline mosquitos of different species found in traps before and after spraying settlements with DDT.

Settlement	Number of traps	Date of spraying	Collection before spraying		Collection after spraying		Species of mosquito	Remarks
			Date	No.	Date	No.		
Hulata	4	10.viii.49	1.viii.49	11	12.viii.49	3	*A. sacharovi*	Breeding site nearby 4 males
					23.viii.49	1		
					31.viii.49	3		
					16.ix.49	6		
					21.ix.49	17		
					29.ix.49	38		
					6.x.49	36		
Yessod Hamaaleh	2	11.viii.49	1.viii.49	22	12.viii.49	7	*A. sacharovi*	
					23.viii.49	1		
					31.viii.49	12		
					16.ix.49	7		
					21.ix.49	14		
					30.ix.49	25		
					5.x.49	23		
Meshek Schwartz	1	1.ix.49	1.ix.49	24	15.ix.49	1	*A. sacharovi*	
					18.ix.49	8		
					27.ix.49	13		
					7.x.49	24		
					11.x.49	29		
Amir	3	15.viii.49	8.viii.49	16	22.viii.49	5	*A. superpictus* 7% *A. sergentii* 2% *A. sacharovi* 91%	7 males Anopheline breeding site in area
					30.viii.49	6		
					12.ix.49	3		
					19.ix.49	11		
					23.ix.49	20		
					4.x.49	54		
					13.x.49	79		
Hulioth	3	16.viii.49	15.viii.49	14	22.viii.49	3	*A. sergentii* 13% *A. superpictus* 18% *A. sacharovi* 69%	
					29.viii.49	4		
					13.ix.49	2		
					19.ix.49	9		
					23.ix.49	17		
					14.x.49	11		
					15.x.49	38		
Shamir	2	22.viii.49	19.viii.49	20	24.viii.49	4	*A. sergentii* 9% *A. superpictus* 40% *A. sacharovi* 51%	
					1.ix.49	2		
					14.ix.49	4		
					20.ix.49	18		
					29.ix.49	22		
					2.x.49	14		
					10.x.49	42		
Kfar Szold	4	23.viii.49	19.viii.49	24	24.viii.49	2	*A. sergentii* 30% *A. superpictus* 20% *A. sacharovi* 50%	
					1.ix.49	3		
					14.ix.49	2		
					20.ix.49	18		
					29.ix.49	16		
					2.x.49	19		
					10.x.49	33		

---

* These data were kindly supplied by Prof. G. Mer, Director of the Antimalaria Research Station, Rosh-Pina.

A trap was placed in a colony in the Beisan valley and observations were made from 23.viii. to 5.ix.39, noting the temperature, humidity and number of mosquitos inside throughout the day. *A. sergentii* adults which inhabit hot, dry zones shift their resting places from time to time during the day, even in such a limited area as a trap, in response to changes in temperature and humidity, the reduction in their numbers towards evening must, of course, be attributed to certain physiological causes. The average number of mosquitos throughout the above-mentioned 14-day period, counted at intervals of two hours without killing them, is shown in fig. 4.

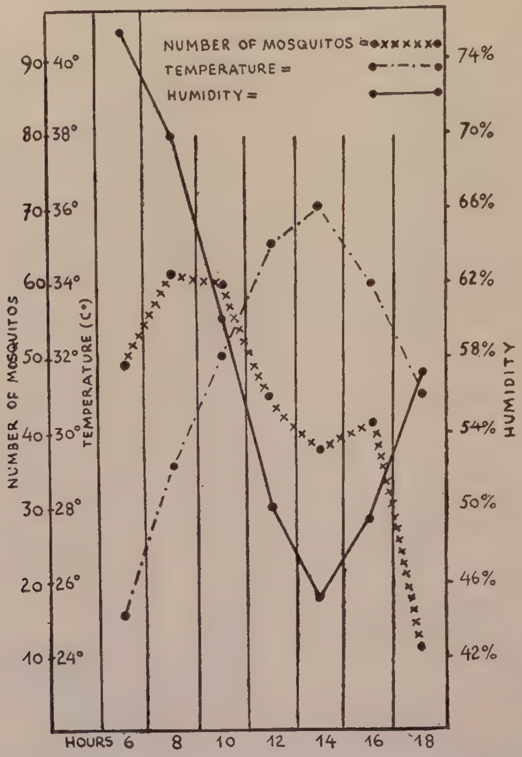


Fig. 4.—Average number of *A. sergentii* in a mosquito trap in Maoz in intervals of two hours during the day and their relation to the temperature and humidity during the period 23.viii. to 5.ix.1939.

On cloudy or dark days the results of the observations were different from those on sunny days. The results of two-hour trap counts, obtained by killing all mosquitos in the trap each time on a cloudy day as compared with a clear day, are shown in Table VII.

The mosquitos enter the trap mostly in the morning hours and may be found there, in their greatest numbers, between 8 and 10. During a cloudy day, however, they may enter freely in the afternoon and only towards evening twilight do they leave the trap. In autumn, with a lower temperature and higher humidity, there is a consequent lowering of the average number of mosquitos entering the trap and instead they are to be found in scattered, sheltered resting places.

Following the extensive use of DDT as a residual spray, great changes have occurred in the resting habits of *A. sergentii*. In 1944, prior to the use of DDT,

TABLE VII.

Numbers of live mosquitos collected in a trap every two hours, between 0600 and 1800 hours, on a clear and on a cloudy day.

(a) Clear day 13.ix.1939							
Hour of count ..	0600	0800	1000	1200	1400	1600	1800
Temperature (°C.) ..	27°	30°	32°	34°	35°	34°	31°
Relative humidity (%)	75	70	60	55	50	52	60
No. of mosquitos ..	15	13	7	1	—	—	—
(b) Cloudy day 15.ix.1939							
Hour of count ..	0600	0800	1000	1200	1400	1600	1800
Temperature (°C.) ..	25°	28°	32°	35°	37°	33°	32°
Relative humidity (%)	78	78	66	56	50	58	63
No. of mosquitos ..	10	8	4	8	1	7	—

the numbers of *A. sergentii* taken from a regular collecting station in a settlement in the Beisan valley, Nir-David, in October, November and December, were 490, 541 and 236, respectively. In 1945, DDT residual spraying was introduced and in September of that year all places where *A. sergentii* had previously been found congregating, *e.g.*, tents, cowsheds and stables, were sprayed. This was concurrent with the usual anti-larval measures in the field. The collecting station counts for the same period were seven mosquitos in four counts in October, ten in six in November and one in one in December.

In 1946 all structures in the settlement were sprayed, once in June and once in September, a single barn being omitted in error. Counts in the regular, sprayed, collecting station and the unsprayed barn showed no mosquitos in October, November or December in the sprayed locations whereas in the unsprayed barn there were 15 in one count in October, 72 in nine in November and 51 in seven counts in December. Searches for adults elsewhere produced only one, found among the grass in a neighbouring field. When a trap was set up in an open field in the Jordan valley, both males and females of *A. sergentii* were found entering freely. In the Dead Sea area, adults were frequently taken marked with the pollen of *Anabasis articulata*, indicating contact with either the flower itself or with the ground beneath these plants (Shapiro, Saliternik & Belferman, 1944). These observations and similar ones in other sprayed areas may indicate that:—

(a) *A. sergentii* is practically eliminated from the sprayed buildings,

(b) *A. sergentii* seeks resting places with unsprayed surfaces,

(c) small numbers of *A. sergentii* may ordinarily be found in the open field.

Adult density variations and flight range.

In the autumn, adults often begin to appear in settlements in waves of varying density at points up to 6·5 km. from their breeding places. Wind appears to be a very important factor in the movement of this species and in the rate of dispersal from a given source.

In the Dead Sea area it was noted (Shapiro, Saliternik & Belferman, 1944) that *A. sergentii* would fly from their breeding sites to a settlement, 6 km. distant, when a gentle night breeze blew from the settlement to the breeding spot. In the Jordan valley, however, it was also noted, by the author, that strong, hot dry easterly winds would blow the mosquitos from their breeding or resting areas to neighbouring settlements. In one settlement intensive search on 16.x.1950 revealed four adult *A. sergentii.* On 10.x.1950 following a night of strong easterly wind of force 5 (Beaufort) more than 100 *A. sergentii* were found in the same settlement and there was a general sharp rise throughout the same area. An increase in the case rate of malaria followed in this area 10 to 14 days later, indicating that many of the mosquitos were already infected when they were blown to the settlement.

A. sergentii may occasionally exchange the open-field resting places, which they apparently prefer, for domestic ones. During the first days of August 1940, the brush cover of a swamp in the Beisan valley, not under malaria control, was burnt over in the course of several days. The variation in the counts in an artificial resting station at a point less than 1 km. distant, following the burn-off, may be seen in Table VIII.

TABLE VIII.

Variation in the number of Anopheline mosquitos in a resting station, caused by burning the swamp brush at the beginning of August 1940.

Date	*A. sergentii*	*A. superpictus*
1.viii.1940	12	5
2.viii.1940	245	30
7.viii.1940	460	80
8.viii.1940	269	44
11.viii.1940	54	13

From the end of September to the end of November there is an increase in the numbers of *A. sergentii* throughout the country, especially in the Jordan valley. This increase is not, however, a gradual one. When the average numbers taken from all collecting stations as well as all other adult resting places are plotted on a graph, sudden ascents and declines may be noted. Such an irregular increase may be seen in fig. 5, illustrating the total daily collections for a site in the Jordan valley during the above-mentioned period, and their apparent lack of relationship to the daily humidity and temperature.

Variations in breeding intensity in the adult population, as well as direct climatic influences, may be the causal factors for the irregularity of this autumn increase, *e.g.*—

(1) Irrigation of the fields is not increasing uniformly throughout the areas and new, localised and temporary artificial breeding spots may be suddenly created by overflow or seepage water.

(2) The emptied irrigation canals dry slowly on account of the increased autumn humidity, often leaving many pools and moist earth sufficiently long for the emergence of a brood or for stranded larvae to survive and complete their development when the canal is refilled.

(3) Sudden wind, and variations in temperature and humidity may cause a shift in preferred resting places of the adults from the open fields to protected sites, including, of course, the collecting stations.

The adult movements and flight range of *A. sergentii* were further investigated in the Dead Sea area in 1942 (Shapiro, Saliternik & Belferman, 1944), 400 m. below sea level. The land is saline and arid, the climate dry and hot and the vegetation, consisting of halophytic bushes, is sparse. There are few human habitations and animals within a distance of five km. from the breeding places. The observations were made in the Fesh'cha swamp in which *A. sergentii* was found breeding in considerable numbers. This is bordered by the Dead Sea on one side and by mountain ranges with numerous caves on the other; the adjacent plains have been characterised above.

In early November, a camp was pitched in the central area of the swamp and nightly collections made of mosquitos coming to feed on men and donkeys. In one night, between 6 p.m. and 8 a.m. the following morning, 14 men made live collections and marked with bronze dust 2,600 mosquitos attempting to bite; these consisted of 2,588 *A. sergentii* (99·6%), 11 *A. superpictus* (0·4%), and 1 *A. multicolor* Camb. (0·04%). In the course of the collecting it was noted that the mosquitos appeared in waves lasting 30 to 45 minutes, their activities then subsiding for intervals of 20 to 30 minutes. As soon as they appeared they bit fiercely, intensifying their activities towards sunrise. The intervals in the waves coincided with a light breeze, when the breeze subsided the mosquitos immediately reappeared. On 6.xi.1942 a further 6,500 *A. sergentii* were collected alive in caves in the hills above the swamp (see Pl. XVIII, fig. 3), caged and also marked with bronze dust. All the mosquitos were liberated the following night from the same spot as those previously marked, and catching was initiated in open fields and buildings 4·2 km. and 6·5 km. distant from the point of release. Between 7.xi.1942 and 7.xii.1942, 3,625 Anophelines were taken at these points. These consisted of 99 per cent. *A. sergentii*, 0·5 per cent. *A. superpictus* and

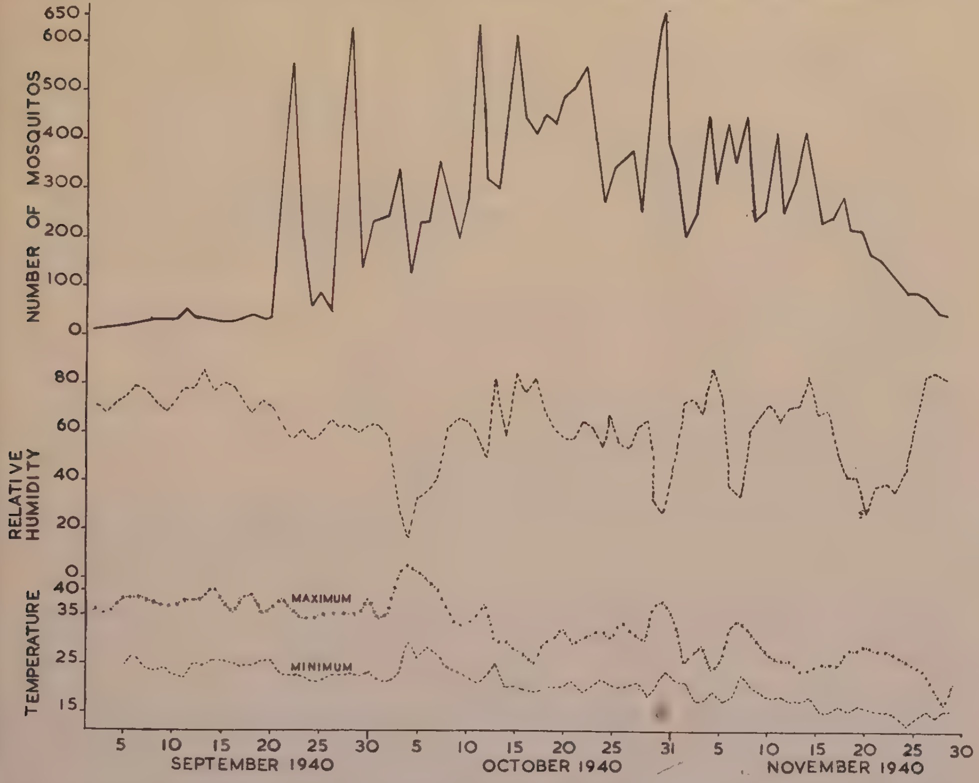


Fig. 5.—Incidence of *A. sergentii* in relation to the daily temperature and humidity in Bet-Zera, a settlement in the Jordan valley, during September–November 1940.

0·5 per cent. *A. multicolor.* Two marked females were recovered or 0·02 per cent. of the number released. The first was taken among 36 other females the night after the release of the mosquitos while biting man in an open field 4·2 km. from the point of release. On 28.xi., a second female of *A. sergentii* was taken in a house 6·5 km. from the point of release. Thus *A. sergentii* is capable of flying at least 6·5 km. in this area.

Of the mosquitos collected for marking, 30 per cent. in the caves and 3·5 per cent. in the field were found to be infested with parasites of the family HYDRACHNIDAE clinging to the thorax or abdomen. Intensive search of fresh water in the entire area, at the point of release, in the vicinity of the collecting points and in the intervening area, revealed these parasites only in the swamps around the release point. Of the mosquitos taken at the 6·5-km. collecting point, 4 per cent. were infested with the parasite, giving further evidence of their ability to fly this distance.

The presence of males does not necessarily indicate the proximity of the breeding place, as is often the case with other Anophelines. In the above-mentioned collections, males at the 6·5-km. collecting point often totalled 30 per cent. of the number collected though there were no breeding places nearer than the point of release.

In flight-range studies in the Huleh valley in 1927, Kligler (1930) determined a similar flight range for *A. sergentii.*

CORRELATION OF CONTROL WORK WITH THE CHARACTERISTICS OF *A. sergentii.*

The aquatic Stages in Swamps.

Macroscopic determination of eggs and larvae.

It was often found desirable to determine the species of eggs or larvae at the breeding site without the aid of a microscope. An examination of 753 Anopheline egg groups in the laboratory and the field (Saliternik, 1945) showed that the eggs of several species, when floating freely together on the surface of a drop of water, will form a pattern characteristic and consistent for the particular species. For instance, eggs of *A. superpictus* always remain parallel to one another on the surface of the water, while those of *A. sergentii* touch each other at an angle. These arrangements can be seen in Plate XVII, figs. 1 & 3.

The larvae, as well, may be in part recognised by macroscopic appearance as well as by their reaction to certain stimuli. Our observations show that if larvae found in the field are placed in a tube with water and the vessel carefully tilted as if to spill the contents, those of *A. sergentii* and *A. superpictus*, which breed in running water, will dart backwards against the current whereas the remaining Anopheline larvae will generally let themselves be carried with the flow.

It is possible to distinguish between larvae of *A. sergentii* and *A. superpictus* by comparing the narrow dark body of the former with the broader, lighter body of the latter. It has already been mentioned (p. 448) that in the presence of *Ceratophyllum* or *Myriophyllum*, *A. sergentii* is occasionally found in association with *A. sacharovi.* These two larvae may also be distinguished, in their last stage, by the questionmark shape assumed by *A. sacharovi* (as well as *A. hyrcanus* (Pall.)) on the surface when disturbed by being blown upon, as compared with the always straight body of *A. sergentii* and the fact that larvae of *A. sergentii*, when disturbed, drop to the bottom, remaining there some time, whereas larvae of *A. sacharovi* will rapidly rise to the surface again.

Antilarval measures.

Periodic drying of stream beds.—This may be done in the case of small streams, creeks and irrigation channels, by diverting the flow into other channels until the old bed dries completely, killing all larvae and pupae. This is only practical in areas where the bed is of such a nature that drying will be rapid and complete. It is apparently the most effective control method for *A. sergentii.*

Drainage, or filling.—In areas of secondary pools, caused by overflow, and in gravel along the banks of wide, shallow streams, drainage and filling is practised to prevent the creation of breeding sites.

Flooding of stream beds.—This is done in order to change the water level, and disperse and eradicate the larvae. Care, however, must be exercised in many of the local shallow streams and irrigation channels that new breeding sites are not created by overflooding, leaving numerous areas of standing water outside the banks when the strong current has receded. When sweeping shallow streams with strong currents it is desirable to introduce malariol with 2 to 5 per cent. DDT at the source by drip cans; when the water level falls, any pools which have been formed at the periphery will then generally be covered by enough oil and DDT to prevent breeding.

Other standard antilarval measures, such as straightening channels to prevent seepage and overflooding, and clearing of aquatic vegetation to permit free flow, are also practised.

Chemical control.

Various oils, by themselves or in combination with the new organic insecticides or paris green, have been used in the control of the aquatic stages. The problem of chemical control of the larvae and pupae is complicated by the currents that are often present in their breeding sites; these may sweep the oils or insecticide away, the larvae resisting the current and clinging to the banks of the stream. For this reason it has been found desirable to spray the banks of the stream, at water level, rather heavily with the control material and thus ensure a gradual seepage of the oil into the current.

Biological control.

Fish (*Gambusia affinis* and *Tilapia*) which have been frequently used, locally, in the control of immature stages of Anopheline mosquitos are of limited success against *A. sergentii* in as much as this species so often breeds in very shallow seepages or overflows where the fish cannot survive.

It has not been found to be practicable to increase the salinity of the breeding places of *A. sergentii*, as the current in its usual breeding sites would rapidly dilute and sweep away the increased salt concentration.

Specific measures against the aquatic stages of *A. sergentii* are not included in the regular schedule of work of the anti-malaria inspectors, because the breeding sites are so often ephemeral in nature and unpredictable in their appearance. Instead, some time is devoted to a search for suspected breeding areas in order to discover and check any new source of breeding which may have developed. These new breeding areas, very often artificial in nature, *e.g.*, overflowing irrigation channels, leaking fish ponds, etc., are treated and then listed for future inspection and treatment should it prove necessary.

The adult Stage.

Determination.

The eggs provide an additional means of separating adults of *A. sergentii* from those of *A. superpictus*, which are frequently found together with them. Living females brought into the laboratory in poor condition, *i.e.*, rubbed, lacking wing or thoracic scales, are retained until it is apparent that the eggs are ready for laying. The eggs are then dissected out and determined by the air floats characteristic of *A. sergentii*, but absent in *A. superpictus*.

Observations on flight movements of adults.

Observations on the flight movements of adults are of importance in connection with specific control:—

(a) to evaluate control work in breeding areas,
(b) to help in determining the direction, type and distance of the breeding place,
(c) to determine the effect of variations in localised climatic or other conditions,
(d) to determine the biological state of the adult (egg development, etc.).

When studying the movements of *A. sergentii*, it was noted that adults begin to leave their resting places indoors at twilight, starting at sunset and continuing for some twenty minutes, collecting on window panes in their attempt to get out of a closed room. If all sources of light in a room were darkened except for one closed window, all the mosquitos in the room would, at twilight, come to that window to escape. They could then be caught, counted and identified. If, during the day, all sources of light in a room were cut off with the exception of a single, closed window, and the room treated with an aerosol containing a very dilute alcoholic extract of pyrethrum, all resting Anophelines would attempt to escape through the lighted window. This phenomenon can be put to use for the rapid recovery and collection of all adults present.

Control of adult mosquitos.

Control of adults of *A. sergentii* is chiefly important in the autumn months, *i.e.*, September to November. Residual control is practised in an area up to 6 km. from breeding places.

Since 1945, when spraying of houses with DDT came into use, it was noted that while *A. sergentii* was affected as much as other species in the sprayed buildings, many of its normal resting sites were often in unsprayed sites such as caves, unfinished buildings, cellars, etc. Therefore to obtain a high degree of residual control the entire surroundings of settlements and villages in the malarial zones are sprayed. Current feeling in Israel, however, is that despite widespread residual spraying, no lessening of effort on larval control can be permitted.

Summary.

Anopheles (*Myzomyia*) *sergentii* (Theo.) has been shown to be the most important vector of malaria, especially of *Plasmodium falciparum*, in Israel at the present time.

The morphology of the adults, larvae and eggs is discussed, details being given of variations in the pigmentation of the fronto-clypeus in the larvae, a factor the possible genetical significance of which is felt to warrant further research.

Resistance of the aquatic stages to extreme variations in environmental conditions and their ability to survive and even metamorphose in minimal amounts of water have been observed. Breeding in nature has been found between 12°C. and 36°C. At 30°C. the time elapsing from egg-laying to hatching is one and a half days. Pupal development takes a further one and a half days and the total time from oviposition to the emergence of the adult is nine days, whereas in winter it may be as much as three months.

In the field, optimum breeding conditions occur in shallow, temporary puddles and seepages, and especially amidst gravel on the banks of wide, shallow streams, at temperatures between 23°C. and 28°C. at an alkalinity of pH 7·0 to 7·5 and salinity up to 0·6 per cent.

Partial shade, either from vertical aquatic vegetation or the banks of streams is characteristic of most breeding places.

A slight increase in numbers of adults of *A. sergentii* is shown in April to June, followed by a decrease and a sudden, great increase between September and November, a peak being reached in October.

Particulars of the adult biology are given. These concern fertility (average—112 eggs per laying), absence of hibernation, resting and hiding behaviour in nature and in a mosquito trap, the seasonal distribution and the flight range (as great as 6·5 km.). *A. sergentii* is described as zoophilic and anthropophilic, resting and biting man and animals indoors and out.

Adaptation of the control methods to the specific characteristics of *A. sergentii* in the aquatic and adult stages is discussed.

Field macroscopic methods are described which facilitate the identification of *A. sergentii* in the egg and larval stages:—

(a) by the aid of the specific pattern of a few eggs on a drop of water,
(b) by the response of the fourth-stage larvae to external stimuli,
(c) by identification of rubbed females through the morphology of their eggs following laying or after dissection in the last stage of their development.

Specific larval control measures are described, *e.g.*, frequent inspection of suspected artificial breeding areas, prevention of seepage and overflooding, diversion of stream flow to other beds to achieve drying of regular bed, and flushing of streams in conjunction with the introduction of malariol and DDT. All these measures are of greatest importance in the autumn.

Control of adults of *A. sergentii* is chiefly important during the months of September to November within a radius of 6·5 km. from the breeding places.

New methods for the collection of adult Anophelines by traps and of those indoors, seeking to escape at twilight, are presented.

Since only partial control is achieved by residual spraying restricted to living quarters, emphasis is placed on widespread residual treatment of all potential resting places, in close connection with regular antilarval measures.

References.

Bodenheimer, F. S. (1926). Über die Voraussage der Generationszahl von Insekten. III.—Z. angew. Ent., **12**, pp. 91–122.

Buxton, P. A. (1924). Applied entomology of Palestine, being a report to the Palestine government.—Bull. ent. Res., **14**, pp. 289–340.

Callot, J. & Ristorcelli, A. (1938). Localité nouvel pour *Anopheles* (*Myzomyia*) *sergenti* Theobald, 1907.—Arch. Inst. Pasteur Tunis, **27**, pp. 105–107.

Kligler, I. J. (1930). The epidemiology and control of malaria in Palestine.—240 pp. Chicago, Univ. Press.

Leeson, H. S., Lumsden, W. H. R., Yofe, J. & Macan, T. T. (1950). *Anopheles* and malaria in the Near East.—Mem. Lond. Sch. Hyg. trop. Med., no. 7, 223 pp.

Mer. G. (1931). Notes on the bionomics of *Anopheles elutus* Edw. (Dipt., Culic.).—Bull. ent. Res., **22**, pp. 137–145.

Mohyddin Farid (1940). Malaria infection in *Anopheles sergenti* in Egypt.—Riv. Malariol., **19**, (1) pp. 159–161.

Saliternik, Z. (1942). The macroscopic differentiation of Anopheline eggs according to their pattern on the surface of water.—Bull. ent. Res., **33**, p. 221.

SALITERNIK, Z. (1945). The biology of the four most important *Anopheles* mosquitoes in Palestine and the adaptation of the antimalaria activities to their specific characteristics.—(Hebrew University doctoral dissertation.)

SALITERNIK, Z. (1950). Annual report of the Antimalaria Department, 1949. [*In Hebrew.*]—Jerusalem, Minist. Hlth.

SALITERNIK, Z. (1953). Report of the Antimalaria Department for 1950–1952. [*In Hebrew with English summary.*]—68 pp. multigraph. Jerusalem, Minist. Hlth.

SHAPIRO, I. I. & SALITERNIK, Z. (1930). Malaria in Palestine. [*In Hebrew.*]—144 pp. Jerusalem, Safer Press.

SHAPIRO, J. M., SALITERNIK, Z. & BELFERMAN, S. (1944). Malaria survey of the Dead Sea area during 1942, including the description of a mosquito flight test and its results.—Trans. R. Soc. trop. Med. Hyg., **38,** pp. 95–116.

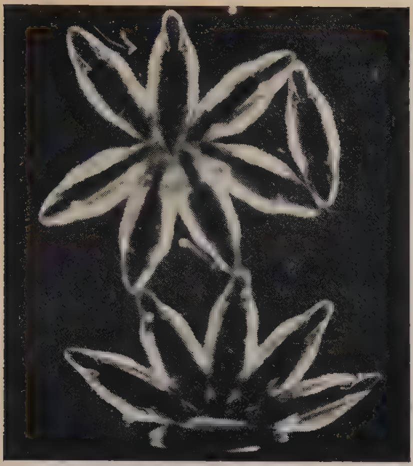


FIG. 1. Pattern of eggs of *A. sergentii* on drop of water.

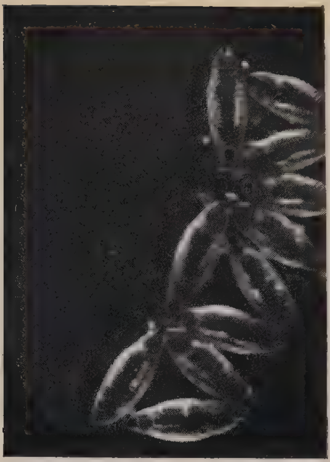


FIG. 2. Eggs of *A. sergentii* exhibiting abnormal structure of exochorion.

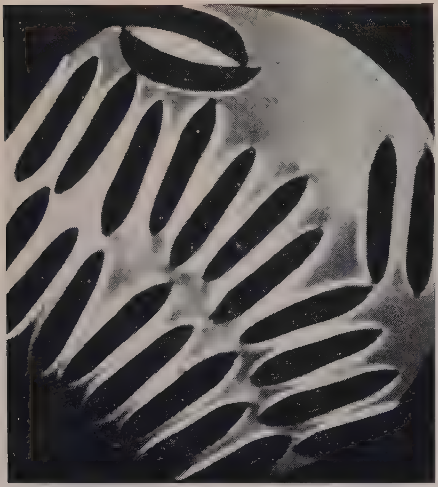


FIG. 3. Pattern of eggs of *A. superpictus* on a drop of water.

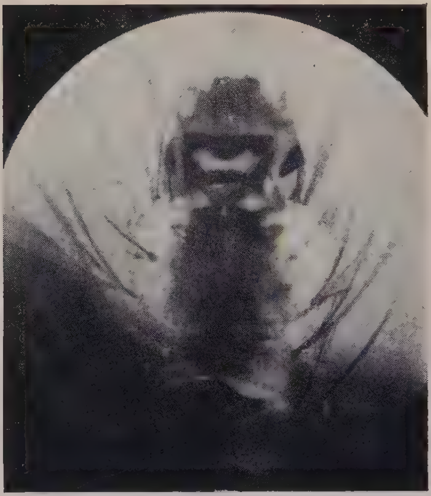


FIG. 4.

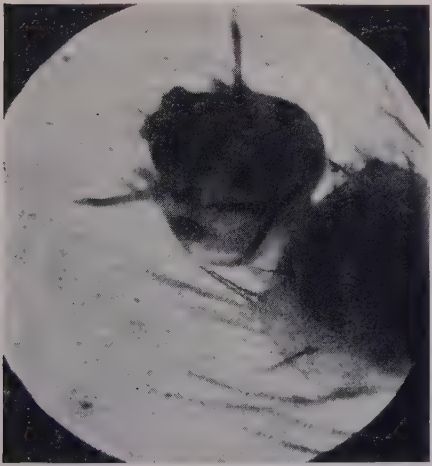


FIG. 5.

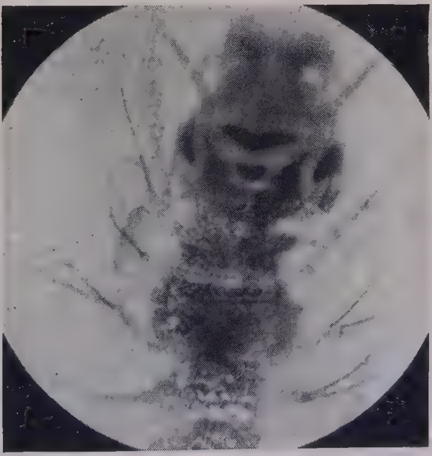


FIG. 6.

FIGS. 4–6. Variations in pigmentation of the fronto-clypeus of larvae of *A. sergentii*.
(4) A continuous transverse band.
(5) A shorter band with small detached lateral spots.
(6) A small transverse band without lateral spots.

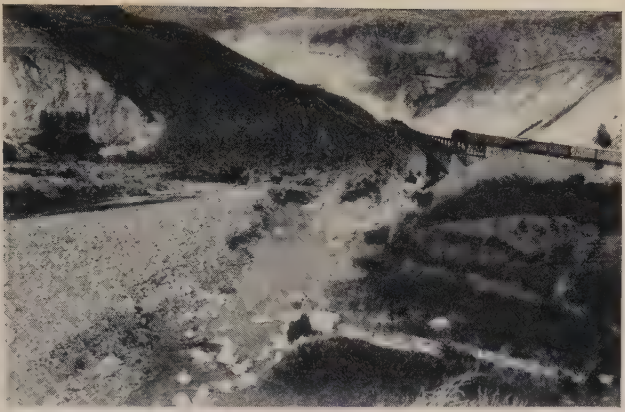


FIG. 1. A typical breeding place of *A. sergentii* in the bed of a wide shallow stream.

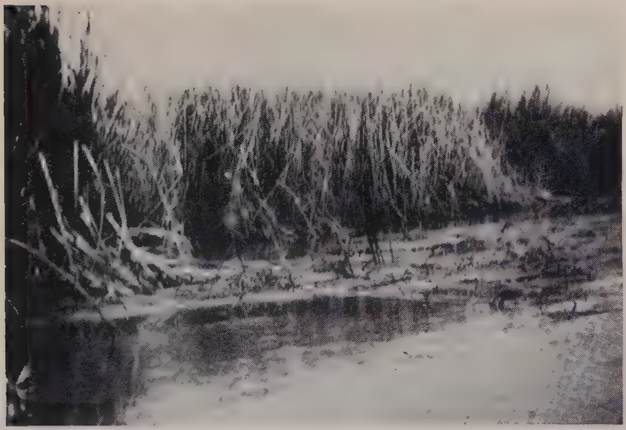


FIG. 2. An equally typical breeding place of *A. sergentii* at the edge of a swamp.

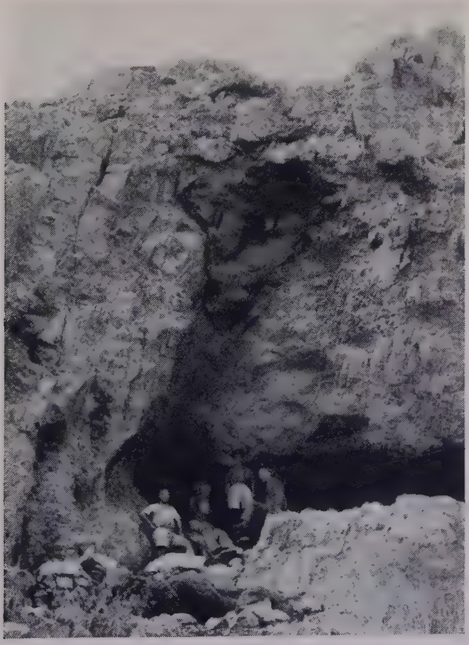


FIG. 3. Cave on the shore of the Dead Sea, where large numbers of adults of *A. sergentii* were taken in 1942.

THE MOSQUITOS OF THE KENYA COAST; RECORDS OF OCCURRENCE, BEHAVIOUR AND HABITAT.

By E. C. C. van Someren, C. Teesdale and M. Furlong
Division of Insect-borne Diseases, Medical Research Laboratory, Nairobi, Kenya.

During the last 12 years the mosquitos of the Kenya coast have been studied in some detail and considerable information collected on their behaviour and distribution. The object of the present paper is to record this information, since our knowledge of the habits of the East African mosquitos is very incomplete and the literature on the subject scanty and inadequate. The method of presentation employed here follows the recent work of Haddow & others (1951).

The data used in this paper have been compiled from records of places where collecting was continued for a year or more and include, from south to north along the coast, Vanga, Msambweni, Mombasa, Takaungu, Kilifi, Gede, Ganda, Malindi and Mambrui, with Rabai about ten miles inland from Mombasa and Kaloleni and Kwale in the hills north and south of Mombasa. With the exception of Ganda, a small inland village near Malindi, the places are well known and marked on any good map. Small collections from a few other places are not included as no unusual species were found.

The coastal region of Kenya lies roughly between 1°30′ S. and 4°30′ S. and is bisected by the meridian 40°00′ E. It is about 280 miles long, with an ill-defined western boundary generally taken to correspond with the 20″ isohyet running 10–20 miles inland and parallel to the coast. The region consists of low-lying country (up to 500 ft.) with small isolated uplifts reaching altitudes of approximately 1,200 ft.

The coastal plain is level or gently undulating and with four permanent rivers and many gullies which hold water in the wet seasons. The soil is light, sandy, porous and sometimes overlies an impervious shale. Along the coast, and a few miles inland, the vegetation consists of shrubs, bush and low grass with patches of indigenous forest; the arid northern and western parts have little cover. The scrub and bush is cleared in patches for the cultivation of maize, sweet potatoes and cotton, and along the coastal strip there are coconut plantations in which are scattered mango, bread fruit, cashew nut and *Citrus* trees and small clearings planted with bananas, pineapple and cassava. There are also a few sisal, sugar-cane and other plantations of recent origin.

The largest hills are those of Kaloleni and Shimba which rise from the plain to elevations of 800–1,200 ft. where the country comprises open undulating grass lands with temporary streams in the valleys, patches of primary and secondary forest and small coconut plantations.

The climate is influenced by the S.E. and N.E. monsoons, the rainfall decreasing from south to north and varying from 50–30 in., with the heavy rains in April and May and showers from June to September. The relative humidity is consistently high throughout the year, averaging 82·5 per cent. The driest and hottest part of the year, from January to mid-March, coincides with the N.E. monsoon. There is no great variation in the temperature, which averages 86·2°F. in the hot and 73·9°F. in the cooler weather, but the hilly parts can be much colder at night and misty in the morning.

In discussing the various species, two collective terms are used to describe the larval habitat; these are (i) " domestic utensils " which includes pots, tins, drums and bottles and (ii) " seed pods " referring to fallen baobab fruits and calabashes. Other larval habitat terms needing definition are " wells ", which are fairly deep and usually lined, " streams " and " rivers ", referring to collections from edges and backwaters and " bamboo pots " which are lengths of bamboo (about 9 in. long) kept filled with water and placed in various situations for the purposes of this investigation.

When describing the habits of the adults, " biting " means that human bait was offered, and here the records are not divided into day and night periods as 24-hr. catches have only recently been carried out systematically. Mosquitos " not biting " are records of routine collections in houses (space spraying and hand-catches) and net-catches in bush. Records " inside " are from huts, labour lines and houses, " bush " catches were done in and around coconut plantations and the " platform " catches were done at Gede in the forest under the canopy.

The terms descriptive of prevalence are those used by Haddow & others (1951) and are as follows: " abundant ", " very common ", " common ", " not uncommon ", " scarce ", " rare " and " very rare ", with " occasional " indicating an irregular occurrence and " exceptional " meaning behaviour outside the normal habits of the species concerned.

A short note and a section on variation is added where the study of a large number of mosquitos has shown variation in ornamentation or of characters used in classification or when it has been found impossible to separate the females or early stages of closely related species.

In addition, the local distribution is given and for this purpose the area has been divided into " highland " (Kwale and Kaloleni) and " coast " (Vanga, Msambweni, Mombasa, Rabai, Takaungu, Kilifi, Gede, Ganda, Malindi and Mambrui). Where a species is not generally distributed this is noted either by naming the places where it is or is not found, whichever is the shorter list. The distribution of the species in East Africa is also included where it is of interest. By East Africa are meant Kenya, Uganda, Tanganyika and Zanzibar.

The species are now discussed and the nomenclature and systematic arrangement follows that used by Edwards (1941) except when pupae are discussed and then the nomenclature used is that of Knight & Chamberlain (1948).

1. **Anopheles (Anopheles) coustani** Lav. s. str.

Coast (except Msambweni and Takaungu) and highland.

Females. *Biting*—in bush, rare; inside, very rare. *Not biting*—in bush and inside, rare.

Males. In bush, very rare.

Variation. Femora and tibiae often broadly yellow below, and sometimes hind tibiae and first tarsal segments creamy white with a dark dorsal stripe from base to near apex; fourth fore-tarsal segments sometimes with a small white apical patch above. Wings with pale areas more extensive than usual but apical spot small; third vein creamy white with few scattered dark scales and a small dark patch at either end.

2. **A. (A.) coustani** var. **ziemanni** Grünb.

Coast (except Vanga, Rabai and Kilifi).

Females. *Biting*—in bush and inside, very rare. *Not biting*—in bush and inside, very rare.

Variation. Tibiae and first tarsal segments often yellow behind for full length (more pronounced on anterior legs).

3. **A. (A.) coustani** var. **tenebrosus** Dön.

Coast (except Vanga, Msambweni, Mombasa and Rabai).

Females. *Biting*—in bush, rare; inside, very rare. *Not biting*—in bush, occasional; inside, rare.

Males. In bush, very rare.

Variation. Wings usually without apical pale spot on costa and fringe spot small.

4. **A. (A.) paludis** Theo.

Coast (Vanga, Mombasa and Ganda only) and highland (Kaloleni only).

Females. *Biting*—in bush, rare. *Not biting*—in bush, rare.

Note. In view of the difficulty of distinguishing the larvae of the *coustani* varieties and *paludis* they have not been recorded separately and the group records are as follows:—

Coast and highland, all localities.

Larvae. *Outside*—swamps and pools, common; streams, drains and dams, occasional; domestic utensils and wells, rare. *Inside*—wells, rare.

5. **A. (A.) implexus** (Theo.).

Coast (Mombasa only).

Larvae. *Outside*—holes, pools, puddles and swamps, very rare.

6. **A. (Myzomyia) nili** (Theo.).

Coast (Msambweni only) and highland (Kwale only).

Females. *Not biting*—inside, very rare.

7. **A. (M.) funestus** Giles.

Coast and highland, all localities.

Females. *Biting*—in bush, occasional; inside, common. *Not biting*—in bush, occasional; inside, abundant.

Males. In bush, scarce; inside, common.

Larvae. *Outside*—wells and swamps, common; seepages, pools, dams and streams, not uncommon; pits, rare. *Inside*—wells and tanks, not uncommon; domestic utensils, occasional.

Variation. Wings with all the usual variation and in addition the apical pale costal spot is often extended to reach the third vein; pre-accessory dark spot on vein one sometimes represented by a few dark scales.

8. **A. (M.) rivulorum** Leeson.

Coast (Malindi and Rabai only) and highland (Kaloleni only).

Larvae. *Outside*—swamps, streams and dams, not uncommon; pools, rock holes and wells, very rare. *Inside*—wells, very rare.

9. **A. (M.) marshalli** (Theo.).

Coast (Msambweni, Mombasa and Kilifi only) and highland.

Females. *Not biting*—inside, very rare.

Larvae. *Outside*—swamps, streams, rivers and pits, very rare.

10. **A. (M.) rhodesiensis** Theo.

Coast (Rabai only) and highland (Kwale only).

Larvae. *Outside*—streams, pools and rock holes, very rare.

11. **A. (M.) keniensis** Evans.

Coast (Kilifi and Rabai only) and highland (Kwale only).

Females. *Not biting*—in bush and inside, very rare.

Larvae. *Outside*—streams and rivers, very rare.

12. **A. (M.) gambiae** Giles.

Coast and highland, all localities.

Females. *Biting*—in bush, not uncommon; inside, common; on platform, rare. *Not biting*—in bush, occasional; inside, abundant.

Males. Inside, common; in bush, occasional.

Larvae. *Outside*—pits, drains, seepages, swamps and pools (rainwater and brackish), common; rock pools, wells, dams, streams, domestic utensils and tanks, occasional. *Inside*—wells, rare; domestic utensils, occasional.

Variation. All the usual variation noted, including specimens with four-banded palps.

Note. Larvae will tolerate a high percentage of sea water and they have been found in large numbers near Malindi, at the top of the Mida creek, where the flat land is regularly flooded by sea water.

13. **A. (M.) maculipalpis** Giles.

Coast (Msambweni, Mombasa and Ganda only) and highland.

Females. Bred material only.

Larvae. *Outside*—swamps, streams, seepages and pools, rare.

14. **A. (M.) pharoensis** Theo.

Coast (Msambweni, Mombasa, Ganda, Malindi and Mambrui only).

Females. *Biting*—in bush, rare. *Not biting*—inside, scarce.

Larvae. *Outside*—pools, scarce; swamps, rare.

15. **A. (M.) squamosus** Theo.

Coast (except Vanga and Takaungu) and highland.

Females. *Biting*—in bush, occasional; inside, rare. *Not biting*—in bush and inside, rare.

LARVAE. *Outside*—dams, swamps and pools, not uncommon; seepages, drains, streams and wells, rare.

VARIATION. Female palps with the two apical white bands sometimes fused. Femora, tibiae and first tarsal joints creamy white behind (first tarsal segments often nearly all white and only faintly speckled in front).

14 16. **Toxorhynchites brevipalpis** (Theo.).

Coast (except Msambweni) and highland.

FEMALES. *Not biting*—in bush, scarce; inside, very rare.

MALES. In bush, rare.

LARVAE. *Outside*—tree holes, not uncommon; domestic utensils and bamboo pots, occasional; pits, rock holes and wells, rare. *Inside*—bamboo pots and domestic utensils, rare.

VARIATION. See van Someren (1946*b*).

17. **T. lutescens** Theo.

Coast (Mombasa, Rabai and Gede only).

FEMALES. *Not biting*—in bush, very rare.

MALES. In bush, very rare.

LARVAE. *Outside*—tree holes, steps cut in coconut palms, seed pods, snail-shells and bamboo pots, rare.

VARIATION. The Mombasa specimens have already been described (van Someren, 1946*b*). Additional characters noted for males from Taveta, Kenya, are as follows: First mid-tarsal segments pale beneath and the second segment of the hind tarsi with a pale blueish-white band near the base; hind tibiae with an indistinct band of post-median white scales.

18. **Uranotaenia alboabdominalis** Theo.

Coast (except Vanga, Msambweni and Gede) and highland (Kwale only).

FEMALES. *Biting*—in bush, once. *Not biting*—in bush and inside, rare.

MALES. In bush, very rare.

LARVAE. *Outside*—swamps, streams and pools, rare; bamboo pots, exceptional.

VARIATION. Femora and tibiae with distinct apical white spots, and pleurae all dark. Much as described by Edwards (1941) for Stanleyville variety but head with a patch of dark scales (black with blue iridescence) on nape.

19. **U. bilineata** var. **fraseri** Edw.

Highland (Kwale only).

FEMALES. *Not biting*—in bush, once only.

MALES. In bush, very rare.

VARIATION. Hind tibiae all dark and last two segments of hind tarsi only faintly paler than the others.

20. **U. balfouri** Theo.

Coast (except Mombasa, Takaungu, Gede and Mambrui) and highland.

FEMALES. *Not biting*—inside, once only.

LARVAE. *Outside*—swamps, not uncommon; streams and pools, rare.

21. **U. candidipes** Edw.

Coast (Rabai only) and highland (Kwale only). Known elsewhere in East Africa only from the Bwamba lowlands, Uganda.

MALES. In bush, very rare.

VARIATION. Head with only a small median patch of dark scales and the third hind-tarsal segment whitish on over the distal half but not quite two-thirds.

22. **U. lucyae** van Someren.

Highland (Kwale only). Not known elsewhere.

FEMALES. *Not biting*—in bush, once only.

MALES. In bush, once only.

23. **U. mashonaensis** Theo.

Coast (Mombasa, Rabai, Kilifi and Malindi only) and highland.

FEMALES. *Not biting*—in bush and inside, very rare.

MALES. In bush and inside, once only.

LARVAE. *Outside*—streams, swamps and pools, rare.

24. **U. nigripes** (Theo.) or **U. fusca** Theo.

Coast (Rabai only).

LARVAE. *Outside*—rock holes, scarce; pools and swamps, rare.

NOTE. Most of the larvae lacked " gills " but when present they were rather short, not more than 2½ times the length of the saddle.

25. **Aëdomyia africana** Nev.-Lem.

Coast (Vanga, Mombasa, Rabai and Ganda only) and highland (Kaloleni only).

LARVAE. *Outside*—streams, dams and pools, rare.

NOTE. Owing to the transparency of the apical fringe the larval comb spines usually appear simple, even under high powers of the microscope.

26. **A. furfurea** (End.).

Coast (Mombasa and Gede only).

FEMALES. *Biting*—in bush, very rare (two specimens only).

VARIATION. One specimen has very few sub-erect scales at base of hind tibiae, no white spots on third wing vein, a small tuft of sub-erect scales on apical corners of tergite 7 and sub-erect scales on apical border of tergite 8. Both specimens have 4–5 small white spots on the first tarsal segments of all legs and the white markings at the base of the wings reduced to small spots.

27. **Ficalbia (Mimomyia) splendens** (Theo.).

Coast (except Takaungu, Ganda and Mambrui) and highland (Kaloleni only).

FEMALES. *Not biting*—in bush, very rare.

LARVAE. *Outside*—dams, swamps, pools and streams, rare.

28. **F. (M.) hispida** (Theo.).

Coast (except Vanga, Msambweni, Mombasa, Rabai and Takaungu) and highland (Kwale only).

FEMALES. *Not biting*—in bush, rare; inside, very rare.

LARVAE. *Outside*—streams, swamps and pools, rare.

VARIATION. First flagellar segment of antennae less than 3 times the length of second. Abdomen with pale lateral spots on tergites large, visible dorsally and those on 5–7 joined to form narrow basal bands.

29. **F. (M.) lacustris** Edw.

Coast (Msambweni and Malindi only).

LARVAE. *Outside*—swamps and pools, rare.

30. **F. (M.) pallida** (Edw.).

Coast (Malindi only). Not known elsewhere in East Africa.

FEMALES. *Not biting*—in bush, once only.

LARVAE. *Outside*—swamps, very rare.

31. **F. (M.) mimomyiaformis** (Newst.).

Coast (except Vanga and Takaungu) and highland.

FEMALES. *Not biting*—in bush, very rare.

MALES. In bush, once only.

LARVAE. *Outside*—swamps, not uncommon; streams, pits and pools, rare; wells, once only.

NOTE. The variety *pincerma* Graham has been recorded from Kilifi (Edwards, 1941).

32. **F. (M.) plumosa** (Theo.).

Coast (except Vanga, Msambweni, Rabai and Takaungu).

FEMALES. *Biting*—in bush, once only. *Not biting*—in bush and inside, rare.

MALES. In bush and inside, very rare.

Larvae. *Outside*—swamps, rare.

Variation. Mid-legs sometimes with the fourth tarsal segments whitish above.

Note. In Kenya, *plumosa* from the inland areas differ from the coastal specimens and Edwards' (1941) description by having not more than the distal third of the third hind-tarsal segments white.

33. **F. (Etorleptiomyia) mediolineata** (Theo.).

Coast (except Mombasa, Rabai and Gede) and highland (Kwale only).

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

Larvae. *Outside*—streams, swamps and pools, rare.

Variation. Legs sometimes very pale with fore- and mid-femora mainly yellow with few scattered black scales and hind femora with 2 large yellow patches on apical half anteriorly. All tibiae mainly yellow with broken dark stripes anteriorly and first tarsal segments sometimes yellow with a narrow black band in the middle but usually dark with a well-defined yellow median patch.

34. **F. (Ficalbia) uniformis** (Theo.).

Coast (Msambweni, Rabai and Malindi only) and highland.

Larvae. *Outside*—streams, rivers, dams, swamps and pools, rare.

35. **Taeniorhynchus (Coquillettidia) metallicus** (Theo.).

Coast (Ganda and Mambrui only).

Females. *Not biting*—in bush, very rare.

36. **T. (C.) maculipennis** (Theo.).

Highland only.

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

Variation. Femora and tibiae with few scattered dark scales and fore- and mid-tarsi with the black markings sometimes greatly reduced. One male has a black ventral line on the proboscis from base to middle.

37. **T. (C.) chrysosoma** Edw.

Coast (Mombasa, Rabai, Ganda, Malindi and Mambrui only) and highland. Taken also at Kiambu, near Nairobi, and Nyeri, Kenya. Not known elsewhere in East Africa.

Females. *Biting*—in bush, very rare. *Not biting*—in bush, very rare.

Males. In bush, rare.

Variation. Proboscis sometimes without any black scales at base. Abdomen usually without black scales above and sometimes lacking the black dot on integument of first tergite. Fore- and mid-tarsi sometimes with the fifth segment all black and fourth segment of mid-legs with a dark line above. Fourth hind-tarsal segment sometimes broadly yellow at base above (males and females).

38. **T. (Mansonioides) africanus** (Theo.).

Coast and highland (Kaloleni only).

FEMALES. *Biting*—in bush, common; inside, rare; on platform, occasional. *Not biting*—in bush, very common; inside, not uncommon.

MALES. In bush, very rare.

LARVAE. *Outside*—swamps, rare.

39. **T. (M.) uniformis** (Theo.).

Coast and highland, all localities.

FEMALES. *Biting*—in bush, common; inside, rare; on platform, rare. *Not biting*—in bush, very common; inside, common.

MALES. In bush, rare; inside, once only.

LARVAE. *Outside*—swamps, rare.

VARIATION. Colour variable, often as dark as *africanus* (with the pale scales white) and sometimes very pale with few dark markings. Mid- and hind-tibiae in particular show great variation (they may be mainly pale with a broken line of dark scales above or the pale areas may be greatly reduced).

40. **Aëdes (Mucidus) scatophagoides** (Theo.).

Coast only.

FEMALES. *Biting*—in bush and on platform, rare; inside, once only. *Not biting*—in bush, occasional; inside, once only.

LARVAE. *Outside*—drains, swamps and pools, occasional; streams and wells, rare.

VARIATION. Abdomen sometimes with two large apical lateral patches of yellow scales on tergites 5–7. Fore- and mid-tarsi usually with the fourth and fifth and sometimes the third segments all yellow.

41. **A. (M.) mucidus** (Karsch).

Coast (Mombasa, Gede and Ganda only).

FEMALES. *Biting*—in bush and on platform, very rare.

LARVAE. *Outside*—drains, swamps and pools, rare.

42. **A. (Mucidus)** species.

NOTE ON UNDESCRIBED SPECIES. These were at first thought to be *A.* (*M.*) *nigerrimus* (Theo.) but on closer examination a number of differences were noted. The main differences are that the scales round the eyes are much narrower than those of *nigerrimus* and the wings have a pale costa. Some of the specimens were sent to Mr. Mattingly of the British Museum who confirmed that they were probably a new species. In view of this it seems worth while to include this mosquito for the sake of completeness, and the records are as follows:—

Coast (Gede and Vanga only). Not known elsewhere.

MALES AND FEMALES. Bred material only.

LARVAE. *Outside*—swamps, very rare.

43. **A. (Ochlerotatus)** species.

NOTE ON UNDESCRIBED SPECIES. This mosquito has been for many years recorded as *A.* (*O.*) *fryeri* (Theo.), the determination being based on female characters only. Recently, males and larvae have been found and these agree very closely with *A.* (*O.*) *dufouri* described by Hamon (1953) but on the evidence of the females this material is not *dufouri* as both claws of the hind legs are simple. The larvae are strikingly different from those attributed to *fryeri* by Hopkins (1952) and it seems probable that this mosquito will prove to be a new species. The records are as follows:—

Coast (except Msambweni, Rabai and Takaungu) and highland. Not known elsewhere.

FEMALES. *Biting*—in bush, scarce; inside, very rare; on platform, rare. *Not biting*—in bush, occasional; inside, very rare.

MALES. In bush, very rare.

LARVAE. *Outside*—salt-water pools, occasional.

44. **A. (Finlaya) fulgens** (Edw.).

Coast (except Vanga and Msambweni) and highland (Kwale only).

FEMALES. *Biting*—in bush, very rare. *Not biting*—in bush, scarce; inside, rare.

MALES. In bush, rare; inside, once only.

LARVAE. *Outside*—tree holes, very common; bamboo pots, scarce; plant axils, seed pods, gutters, rock holes and steps cut in coconut palms, rare; snail-shells, tins and wells, exceptional. *Inside*—bamboo pots, very rare.

VARIATION. Leg markings very variable. Fore-femora very often with a silvery line below on basal two-thirds; anteriorly, mid-femora usually with a basal silvery ventral line meeting the median silvery spot which is sometimes absent; silvery patch on hind femora occupies about middle third of anterior surface. Fore-tibiae often white or pale blue below and hind-tibiae sometimes with narrow white basal rings. Fore-tarsi with the first and second segments all white behind or second white only on the basal half; mid-tarsi with the first segment all white or with a dark line in front, the second may be black anteriorly on the apical half and the third sometimes behind basally and occasionally nearly all white; first hind-tarsal segment sometimes with a very small basal silvery spot above. Abdomen sometimes with very small or no paired sub-dorsal silvery spots on seventh tergite.

45. **A. (F.) ingrami** Edw.

Coast (Gede only) and highland (Kwale only).

MALES. In bush, once only.

LARVAE. *Outside*—tree holes, rare.

46. **A. (Stegomyia) aegypti** (L.).

Coast and highland, all localities.

Females. *Biting*—on platform, rare.

Larvae. *Outside*—tree holes, domestic utensils, tanks, coconut-shells and bamboo pots, common; plant axils, wells, rock holes and steps cut in coconut palms, scarce; ground pools, exceptional. *Inside*—domestic utensils, abundant; bamboo pots, common; wells, not uncommon; puddles on floor, occasional.

Note. Although a great deal of variation was noted in the colour of this species the pale and dark forms were not differentiated in the earlier records. Latterly, an attempt was made to separate the pale form (var. *queenslandensis* (Theo.)) and the dark form (*aegypti* s.str.). It appears from these records that the pale form is mainly house haunting and the dark form is usually found in the bush. The biting records given below are based on a year's collecting at Rabai and the non-biting records from space spraying in the Ganda area.

aegypti (L.) s. str.

Females. *Biting*—in bush, rare; inside, scarce. *Not biting*—in bush, scarce; inside, rare.

Males. In bush, scarce; inside, rare.

Variation. Many hundreds of specimens bred from larvae taken from containers in the bush at Ganda were consistently dark (black with white markings). The following colour variation was noted: White bands on abdominal tergites usually well marked, rarely narrow, much reduced or absent; first tergite usually all black above but sometimes with a small spot of white scales medianly. Hind-tarsal segments 1–3 white on basal one-third to one-fourth, fourth on basal three-quarters and fifth all white.

var. **queenslandensis** (Theo.).

Females. *Biting*—inside, common. *Not biting*—in bush, very rare; inside, not uncommon.

Males. Inside, scarce.

Variation. Ground colour of scutum dark brown to pale yellow. Head with the vertex sometimes mainly pale but usually with a small patch of dark scales on either side or rarely with lateral dark patches large. First abdominal tergite usually with a large patch of white scales above, other segments lightly or heavily sprinkled with white scales or rarely nearly all white; occasionally tergites dark with narrow apical white bands only or more often with broad apical and basal white or yellowish bands and rarely with pale bands very indistinct. Hind tarsi usually as described above but sometimes fourth segment with a narrower white basal ring and the fifth often has a dark band at tip.

47. **A. (S.) subargenteus** Edw.

Coast (Ganda only). Found also at Taveta, Kenya. Not known elsewhere in East Africa.

Females. *Biting*—in bush, very rare. *Not biting*—in bush, scarce.

Variation. Head with the black patches on vertex large or small and scales on nape not always yellowish; one specimen has a broad band of black scales across the front of the head and the scales on the nape white with a yellowish tint.

48. **A. (S.) woodi** Edw.

Coast (Rabai and Ganda only) and highland (Kaloleni only). Known also from Kakuyuni near Ganda and Witu, Kenya coast, and Tengeni, Tanganyika (P. F. Mattingly, private communication). Not known elsewhere outside Nyasaland.

Females. *Biting*—in bush, not uncommon; inside, very rare. *Not biting*—in bush, common; inside, rare.

Males. In bush, very rare.

Variation. Black lateral patches on head large or small. Lateral lobe of scutellum sometimes with a few silvery scales and mid-lobe usually with a patch of black scales at apex. Abdomen occasionally with a narrow silvery basal band on second tergite.

49. **A. (S.) simpsoni** (Theo.).

Coast and highland, all localities.

Females. *Biting*—in bush, common; inside, scarce; on platform, once only. *Not biting*—in bush, common; inside, rare.

Males. In bush and inside, rare.

Larvae. *Outside*—plant axils and bamboo pots, common; coconut-shells, tree holes and tins, scarce; snail-shells, domestic utensils, gully traps and roof gutters, exceptional. *Inside*—bamboo pots and domestic utensils, rare.

Variation. Median yellow lines on scutum occasionally reaching to front margin, more often not extended beyond a half and sometimes absent. Fore-femora usually with a white line below on basal half. First two segments of fore-tarsi sometimes extensively white behind; mid-tarsi with the first two segments often white behind to near tip but second segment sometimes black all round on apical half; fourth hind tarsal segment occasionally with a small white spot at base above and fifth segment sometimes with a black tip. Claws of anterior legs of female toothed (considerable number examined for this character).

50. **A. (S.) metallicus** (Edw.).

Coast and highland, all localities.

Females. *Biting*—in bush, not uncommon; inside, very rare; on platform, rare. *Not biting*—in bush, not uncommon; inside, rare.

Males. In bush, scarce; inside, very rare.

Larvae. *Outside*—bamboo pots, common; tree holes, not uncommon; coconut-shells, domestic utensils, gutters and plant axils, scarce; snail-shells, steps cut in coconut palms, rare. *Inside*—domestic utensils, rare.

Variation. Fore- and mid-femora often with a broken line of silvery scales below from base to beyond a half; fore-femora sometimes without a silvery spot at tip below and hind femora often with the whole of the anterior surface silvery on basal half. Fore- and mid-tibiae sometimes with a yellow line below and hind tibiae often with a small basal white spot below.

51. **A. (S.) apicoargenteus** (Theo.).

Coast (Ganda only).

FEMALES. *Not biting*—in bush, very rare.

52. **A. (S.) dendrophilus** Edw.

NOTE ON UNDESCRIBED SUB-SPECIES. Specimens of this mosquito were sent to Mr. Mattingly, at the British Museum, and he is of the opinion that they clearly represent a distinct sub-species (Mattingly, 1953). They are easily distinguished by the markings of the mid-tarsi, the first three segments being broadly white behind. The records are as follows:—

Highland (Kwale only). Not known elsewhere.

FEMALES. *Not biting*—in bush and inside, very rare.

MALES. In bush, very rare.

LARVAE. *Outside*—bamboo pots, scarce; tree holes, rare.

53. **A. (S.) heischi** van Someren.

Coast (except Msambweni and Kilifi) and highland.

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, rare; inside, very rare.

MALES. In bush, very rare.

LARVAE. *Outside*—tree holes and bamboo pots, common; steps cut in coconut palms, plant axils, coconut-shells and seed pods, occasional; domestic utensils and wells, exceptional. *Inside*—bamboo pots, rare.

54. **A. (S.) calceatus** Edw.

Coast (except Msambweni and Malindi) and highland.

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, rare.

MALES. In bush, very rare.

LARVAE. Bred material from bamboo pots, coconut-shells, tins and tree holes.

VARIATION. Hind femora sometimes with the basal third of anterior surface white, followed by a black patch and a large silvery spot at a half. Mid-tibiae sometimes with a narrow white ring at the base. Fore-tarsi with the first segment sometimes all white and second occasionally white behind, on basal half; mid-tarsi with the first segment dark in front for nearly the whole length or only on apical half, second often all white with only a small black spot at tip and third sometimes all black; third hind-tarsal segment with the basal band often very narrow. Abdomen sometimes with only a small basal white patch on third tergite.

55. **A. (S.) soleatus** Edw.

Coast (Vanga, Rabai, Gede and Ganda only) and highland (Kwale only).

Females. *Biting*—in bush, very rare. *Not biting*—in bush, very rare.

Males. In bush, rare.

Larvae. Bred material from bamboo pots and tree holes.

Variation. Posterior median white line on scutum sometimes continued forward to near front margin (male). Abdomen without white basal bands on tergite 2 (usually) and 3 (sometimes). Mid-tarsi usually with segments 1–4 extensively white behind and above and with a variable amount of black scaling in front or 3 and 4 may be all black.

Note. Owing to the difficulty of separating the larvae of *apicoargenteus*, *calceatus* and *soleatus* the larvae have been recorded under one heading and the records are as follows:—

Larvae. *Outside*—tree holes and bamboo pots, common; steps cut in coconut palms, coconut-shells, seed pods, snail-shells and rock holes, rare; plant axils, exceptional.

56. **A. (S.) vittatus** (Big.).

Coast (except Msambweni, Gede and Ganda) and highland (Kwale only).

Females. *Biting*—in bush, rare; inside, very rare. *Not biting*—in bush, scarce; inside, very rare.

Males. In bush, very rare.

Larvae. *Outside*—drainage canals, common; rock holes, not uncommon; tanks, scarce; swamps, pools, pits, streams, seepages, gully traps and domestic utensils, rare; wells and dams, very rare; steps cut in coconut palms and tree holes, exceptional. *Inside*—domestic utensils, once only.

57. **A. (Aëdimorphus) ngong** van Someren.

Coast (Gede only). Found also in the Langata forest near Nairobi, Kenya. Not known elsewhere.

Males and Females. Bred material only.

Larvae. Obtained by filling dry tree holes in forest.

Variation. Larval comb scales narrow or broad with long or short fringes.

Note. The record of *A. ngong* is supplied by Dr. W. H. R. Lumsden of the Virus Research Institute, Entebbe.

58. **A. (A.) haworthi** Edw.

Coast (except Vanga and Malindi) and highland.

Females. *Biting*—in bush, very rare; inside, once only. *Not biting*—in bush, very rare.

Males. In bush, very rare.

Larvae. Bred material from steps cut in coconut palms and tree holes.

Variation. Occasionally a pair of yellow spots, composed of narrow scales, about the middle of the scutum; posterior lateral white lines on scutum may be absent or indicated by lines of narrow yellow scales but sometimes mainly composed of broad scales. Second segment of fore- and mid-tarsi sometimes all dark but usually with small white apical spots; banding of hind tarsi variable, third and fourth segments a little less or over a half white. All tibiae sometimes broadly or narrowly buff behind. Larval comb scales may be broad with short or long fringes.

59. **A. (A.) teesdalei** van Someren.

Coast (Vanga and Ganda only) and highland (Kwale only). Not known elsewhere.

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

Larvae. Bred material from bamboo pots and tree holes.

Note. Owing to the variation found in the comb scales of *A. haworthi* it is not possible to use this character (van Someren, 1946*a*) to separate this larva from *A. ngong* and *A. teesdalei* which are also indistinguishable. The combined larval records are as follows:—

Larvae. *Outside*—steps cut in coconut palms, not uncommon; tree holes and bamboo pots, scarce; plant axils and seed pods, exceptional. *Inside*—bamboo pots, once only.

60. **A. (A.) argenteopunctatus** (Theo.).

Coast and highland, all localities.

Females. *Biting*—in bush, very rare. *Not biting*—in bush, occasional; inside, once only.

Males. In bush, very rare.

Larvae. *Outside*—swamps and wells, occasional; drains and pits, rare; tree holes and domestic utensils, exceptional.

61. **A. (A.) domesticus** (Theo.).

Highland (Kwale only). Not known elsewhere in East Africa outside Uganda.

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

Variation. Hind femora with the white spot at three-quarters small and practically all dorsal. Hind tibiae with the dorsal apical white patch occupying about a third the length of the tibia. Male terminalia with two short stout hairs at tip of basal lobe (one longer than the other).

62. **A. (A.) leptolabis** Edw.

Highland (Kaloleni only). Not known elsewhere in East Africa outside Uganda.

Males. In bush, once only.

Variation. Abdomen with no basal white bands on tergites. Fore- and mid-legs with large apical white spots on tibiae but none on femora; about apical fourth of hind tibiae white dorsally. Male terminalia with the basal lobe of coxites covered with short fine hairs and with a long hair about the middle on the inside and two short spines at the tip.

63. **A. (A.) tarsalis** (Newst.).

Coast (except Msambweni, Kilifi, Gede and Malindi) and highland.

Females. *Biting*—in bush, rare. *Not biting*—in bush, occasional.

Males. In bush and inside, rare.

Larvae. *Outside*—streams and wells, very rare; drum, exceptional. *Inside*—domestic utensils, once only.

64. **A. (A.) albocephalus** (Theo.).

Coast and highland, all localities.

Females. *Biting*—in bush, not uncommon; inside, very rare. *Not biting*—in bush, common; inside, rare.

Males. In bush, not uncommon; inside, rare.

Larvae. *Outside*—wells and swamps, not uncommon; drains, rare; tins and tree holes, exceptional.

Variation. All lobes of scutellum with narrow yellow scales which are usually very narrow but sometimes those on lateral lobes slightly broader. Scutum with the yellow scales often forming an indefinite pattern; scales on post- and sub-spiracular areas and paratergites usually smaller and narrower than the other pleural scales and sometimes quite narrow. Fore- and mid-tibiae with a full-length creamy line below. Wings with a line of pale scales at base of costa below. Male terminalia sometimes with a few fine hairs on upper fork of style.

Note. It is sometimes difficult to separate the females of *albocephalus* and *tarsalis* (Haddow & others, 1951) but here they have been recorded separately and the character of the scales on the scutellum has been used to determine the species. Although only a few male *tarsalis* have been collected all those seen had broad silvery scales on all lobes of the scutellum. No such scales have ever been seen on the *albocephalus* from this area.

65. **A. (A.) tricholabis** Edw.

Coast (except Vanga, Msambweni and Kilifi) and highland. Known elsewhere only from the Bwamba lowlands, Uganda.

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

Larvae. *Outside*—swamps, very rare.

Note. The larvae recorded here as this species agree with the description of ssp. *bwamba* (van Someren, 1950*b*). Additional characters noted are as follows: Antennae dark on about apical two-thirds and with a tuft of about 8 plumose branches. Siphonal index a little over 3; pecten with up to 20 spines, extending over a half and sometimes the last 3 spines are wider spaced. "Gills" less than twice the length of the saddle.

66. **A. (A.) abnormalis** ssp. **kabwachensis** Edw.

Coast (Rabai, Takaungu, Ganda, Malindi and Mambrui only) and highland.

MALES. In bush, very rare.

67. **A. (A.) leesoni** ssp. **verna** Lewis.

Coast (Mombasa, Rabai, Takaungu, Ganda and Mambrui only) and highland. Taken also at Garissa on the Tana river, Kenya. Not known elsewhere outside the Anglo-Egyptian Sudan.

MALES. In bush, very rare.

LARVAE. *Outside*—swamps and streams, very rare.

VARIATION. Larval antennal tuft at a half and with 4–5 stiff, sparsely-plumose branches. Head seta A with 4–6 and B and C with 2–3 branches. Siphonal index 5 and pecten not extending to near a half, with 14–17 spines and the last 2 or 3 wider spaced and simple. Upper caudal seta with 9–11 branches.

NOTE. Owing to the difficulty of distinguishing mosquitos of the *abnormalis* group (as defined by Edwards, 1941) except by the examination of male terminalia, the female records refer to the group rather than to any particular species. These group records are as follows:—

Coast (Vanga, Takaungu, Ganda, Malindi and Mambrui only) and highland (Kaloleni only).

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, scarce.

68. **A. (A.) lamborni** Edw.

Coast (Rabai only).

LARVAE. *Outside*—tree hole, once only.

69. **A. (A.) cumminsi** ssp. **holocinctus** Edw.

Coast (Gede only).

MALES. In bush, once only (Edwards, 1941).

70. **A. (A.) cumminsi** ssp. **mediopunctatus** (Theo.).

Coast (except Msambweni, Takaungu and Gede) and highland.

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, scarce.

MALES. In bush, very rare.

VARIATION. Abdomen with the median basal spots on the tergites quite large or very small and often absent on the last few segments; sternites sometimes unbanded but with dark apical lateral spots. Hind femora sometimes dark anteriorly below on distal fourth.

NOTE. Larvae of *A. cumminsi* have been taken in small numbers. The records are as follows:—

LARVAE. *Outside*—swamps and wells, rare.

71. **A. (A.) hirsutus** (Theo.).

Coast (Gede and Malindi only).

Females. *Not biting*—in bush and inside, very rare.

Larvae. *Outside*—swamps, very rare.

72. **A. (A.) fowleri** (Charmoy).

Coast (Kilifi only).

Females. *Not biting*—inside, once only.

Larvae. *Outside*—swamps, very rare.

73. **A. (A.) ochraceus** (Theo.).

Coast (Mombasa, Kilifi, Ganda and Malindi only) and highland (Kaloleni only).

Males and Females. Reared material only.

Larvae. *Outside*—pools, swamps and pits, rare; domestic utensils, exceptional. *Inside*—bamboo pots, once only.

Variation. Fore-tibiae sometimes with the median yellow stripe very narrow and ill defined and with scattered pale scales in the dark areas or occasionally all yellow with a distinct dark line or only a few scattered dark scales above. Upper dark line of mid-tibiae sometimes broken and lower of hind tibiae sometimes absent. Hind femora sometimes with the dark dorsal line broken.

74. **A. (Banksinella) albothorax** (Theo.).

Coast (except Msambweni, Kilifi, Gede and Malindi) and highland.

Females. *Biting*—in bush, common; inside, very rare. *Not biting*—in bush, common.

Males. In bush, scarce.

Larvae. Bred material from swamps.

Variation. Pale scales on head and thorax creamy white and sometimes addition: Tori dark brown or pale and darkened on the inside. Scutal scales creamy or whitish. Tergites usually with basal and sometimes apical lateral patches with or without connecting yellow lines, sometimes with no lateral yellow patches and occasionally with broad yellow lateral borders; sternites pale or dark or mottled and sometimes dark with basal lateral yellow patches. All tibiae pale below and sometimes broadly yellow; mid- and hind-tibiae occasionally yellow with a few scattered dark scales above or hind tibiae entirely pale yellow on the apical half; mid-tibiae usually without apical pale spots. Wings with the apical third of the costa often paler than the basal half but not definitely white or yellow; first vein pale on the basal one-third to two-thirds; fifth vein sometimes pale to near tip.

Note. *Banksinella* larvae have occasionally been taken from swamps, wells and streams.

75. **A. (B.) albicosta** (Edw.).

Coast and highland, all localities.

FEMALES. *Biting*—in bush, not uncommon; inside, very rare. *Not biting*—in bush, not uncommon; inside, rare.

MALES. In bush, scarce.

VARIATION. Pale scales on head and thorax creamy white and sometimes pale yellow. The proboscis may be only indistinctly pale below or the pale scales may extend up the sides leaving only a narrow dark dorsal line. Abdomen with lateral spots on tergites large or small, never joined and occasionally the apical spots are absent; sternites dark but often with small basal lateral spots of pale scales. All tibiae pale behind with the fore-tibiae sometimes pale all round at apex; hind tibiae may be mottled above and sometimes dark above at apex. Wings with the first vein pale on less than the basal half but sometimes pale to tip with the apical half mottled.

76. **A. (B.) flavimargo** Edw.

Coast (Gede only). Not known elsewhere.

FEMALES. *Not biting*—in bush, once only (Edwards, 1941).

77. **A. (B.) ellinorae** Edw.

Coast (except Vanga, Msambweni and Rabai). Not known elsewhere.

FEMALES. *Not biting*—in bush, very rare.

MALES. In bush, rare.

78. **A. (Diceromyia) furcifer** (Edw.).

Coast (Gede only).

MALES. In bush, rare; on platform, not uncommon.

VARIATION. Abdomen with the yellow scales on tergites forming apical lateral patches. Fore- and mid-tarsi with only three white bands.

79. **A. (D.) taylori** Edw.

Coast (Takaungu and Gede only) and highland (Kwale only).

MALES. On platform, fairly common.

LARVAE. Bred material from tree holes.

VARIATION. Yellow and black scales on scutum often forming definite but variable patterns. Abdomen with the tergites heavily sprinkled with yellow scales, usually forming apical lateral patches. First tarsal segments of fore- and mid-legs and fore-tibiae sometimes all white behind and occasionally only three white bands on anterior tarsi. The larval comb spines appear simple even under high powers of the microscope but a very short, fine basal fringe can sometimes be seen on one or two spines in each comb. In other respects they are similar to the South African specimens described in Hopkins (1952).

NOTE. According to Edwards (1941) *taylori* differs from *furcifer* by lacking or having very few yellow scales on the abdominal tergites. As seen from the above notes this character is very unreliable and the species can be distinguished only on examination of the male terminalia. The records for the females of these two mosquitos and for the larvae, which are also indistinguishable, are as follows:—

Females. *Biting*—in bush, rare; on platform, common. *Not biting*—in bush, once only.

Larvae. *Outside*—tree holes, common; pineapple tops and steps cut in coconut palms, very rare.

80. **A. (D.) adersi** (Edw.).

Coast and highland, all localities.

Females. *Biting*—in bush, rare; on platform, not uncommon. *Not biting*—in bush, scarce; inside, rare.

Males. In bush, very rare; on platform, not uncommon.

Larvae. *Outside*—bamboo pots, not uncommon; tree holes, coconut-shells and steps cut in coconut palms, occasional; domestic utensils, exceptional.

Variation. White basal bands on tergites sometimes broken on either side of mid line. Male palpi with scattered light scales between the basal bands on shaft.

81. **A. (Dunnius) michaelikati** van Someren.

Coast (Rabai, Gede, Ganda and Mambrui only) and highland. Found also at Taveta, Kenya. Not known elsewhere.

Females. *Biting*—in bush, very rare. *Not biting*—in bush, rare.

Males. In bush, rare.

Larvae. *Outside*—bamboo pots, common; tree holes, scarce.

Variation. Fifth tergite sometimes without a narrow white band joining lateral patches.

82. **A. (Skusea) pembaensis** (Theo.).

Coast and highland, all localities.

Females. *Biting*—in bush, abundant; on platform, rare. *Not biting*—in bush, very common; inside, not uncommon.

Males. In bush, not uncommon; inside, scarce.

Larvae. *Outside*—crab-holes, common; pools and swamps, rare; bamboo pots, tree holes and domestic utensils, exceptional.

83. **Eretmapodites subsimplicipes** Edw.

Coast (except Msambweni) and highland.

Females. *Biting*—in bush, not uncommon. *Not biting*—in bush, common.

Males. In bush, not uncommon; inside, very rare.

Larvae. Bred material from coconut-shells, tins, tree holes and bamboo pots.

VARIATION. Scutal integument usually bright orange but occasionally very dark (almost brown); scutum often with very few yellow scales. Yellow markings on hind femora variable (van Someren, 1949). Male palpi much shorter than proboscis.

NOTE. So far all the adults of the *chrysogaster* group taken in this area have been *subsimplicipes* and it seems probable that the larval records are of this species only but owing to the difficulty of distinguishing the early stages (Haddow, 1946) the larvae have been recorded under a group heading. The records are as follows:—

LARVAE. *Outside*—coconut-shells, bamboo pots and fallen leaves, common; tree holes, plant axils and snail-shells, not uncommon; domestic utensils and rock holes, very rare; swamps and pools, exceptional. *Inside*—domestic utensils, very rare.

84. **E. silvestris** ssp. **conchobius** Edw.

Coast (except Msambweni) and highland.

FEMALES. *Biting*—in bush, scarce. *Not biting*—in bush, scarce.

MALES. In bush, rare.

LARVAE. *Outside*—tins and bamboo pots, not uncommon; coconut-shells, snail-shells and seed pods, scarce; plant axils and tree holes, rare.

VARIATION. Integument of pleurae often dark under silvery stripe and hind femora sometimes yellow on the basal two-thirds anteriorly. Larval comb spines very variable, sometimes long and narrow with a fine basal fringe of denticles or short and broad with coarse basal denticles. Pecten spines sometimes arranged in two parallel lines and subventral tuft sometimes single. Ventral brush may have all four setae single with one or two shorter than the others or the shorter setae may be bifid or divided distally into 3–4 branches. Pupae with hair 2 on second tergite sometimes single and hair 8 with 2–6 and 3–8 branches on tergites VII and VIII respectively; paddles may be a little longer than broad.

85. **E. inornatus** Newst.

Coast (Gede only).

LARVAE. *Outside*—bamboo pots, once only.

86. **E. quinquevittatus** Theo.

Coast (except Msambweni) and highland.

FEMALES. *Biting*—in bush, not uncommon. *Not biting*—in bush, scarce; inside, very rare.

MALES. In bush, scarce.

LARVAE. *Outside*—tanks, common; snail-shells, gully traps and plant axils, not uncommon; bamboo pots, rock holes and bottles, rare.

VARIATION. Width of yellow lines on scutum variable and sometimes quite narrow but never as narrow as those on the scutum of *inornatus*. The lateral yellow lines usually reach to about the middle of the humeral area but occasionally not reaching much beyond shoulders and sometimes continuing forward narrowly to the front margin. Distal claspettes of male terminalia with a row of hairs on internal border and round tip (distal hairs stouter than the rest and curved) and with two sub-apical sigmoid hairs with harpoon-like tips. All larvae seen differ from the description given by Hopkins (1952) by having 1–5 (usually 1) sharp pointed pecten spines, each spine having 2–3 fine ventral and sometimes one or two dorsal denticles (occasionally they appear simple and may apparently be absent); subventral tuft single, stout and sparsely plumose. Saddle with lateral seta 3–5-branched. Seta B of segment VIII plumose.

NOTE. The identity of the larvae was confirmed by bred material (males and females).

87. **E. oedipodius** ssp. **parvipluma** Edw.

Coast (Mombasa only) and highland (Kwale only).

FEMALES. Reared material only (Edwards, 1941).

LARVAE. *Outside*—fallen leaves and bamboo pots, very rare.

88. **Culex (Lutzia) tigripes** Grp.

Coast and highland, all localities.

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, occasional; inside, very rare.

MALES. In bush, occasional.

LARVAE. *Outside*—wells and swamps, not uncommon; tree holes, plant axils, domestic utensils, bamboo pots, tanks, pools, rock holes, drains, pits and streams, rare. *Inside*—domestic utensils and wells, rare.

VARIATION. Two forms seen (1 and 3 described by Edwards, 1941). Apical yellow bands of tergites, when present, often narrow and sometimes broadly interrupted in the middle; sternites 5–7 often with fairly large dark apical patches.

89. **C. (Neoculex) insignis** (Cart.).

Coast (except Vanga and Msambweni) and highland.

FEMALES. *Not biting*—in bush, very rare; inside, very rare.

MALES. In bush, very rare.

NOTE. Larvae recorded as *C. sunyanensis* Edw. probably refer to this species. The record is as follows:—

LARVAE. *Outside*—edge of furrow, once only.

90. **C. (N.) wigglesworthi** Edw.

Coast (Mombasa, Takaungu, Gede and Ganda only) and highland.

FEMALES. *Not biting*—in bush and inside, very rare.

MALES. In bush, rare; inside, once only.

LARVAE. *Outside*—streams and swamps, scarce; tree holes, once only.

91. **C. (N.) albiventris** Edw.

Coast (Mombasa, Gede and Malindi only).

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

92. **C. (N.) adersianus** Edw.

Coast (Mombasa, Rabai, Gede and Malindi only) and highland (Kwale only).

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

Larvae. *Outside*—tree holes, scarce; wells and bamboo pots, rare.

93. **C. (N.) horridus** Edw.

Coast (except Mambrui) and highland.

Females. *Biting*—in bush and inside, very rare. *Not biting*—in bush and inside, occasional.

Males. In bush and inside, occasional.

Larvae. *Outside*—tree holes, not uncommon; bamboo pots, coconut-shells and steps cut in coconut palms, occasional; seed pods, pits, wells, tanks, rock holes and tins, rare.

Variation. Head sometimes with flat white scales at sides and pale yellowish-brown erect scales. Scutal integument sometimes light yellowish-brown and with scales of the same colour and sometimes with a band of narrow white scales round the front margin; *ppn* with a line of narrow white scales above and sternopleural scales sometimes absent. Larval head setae B and C may be single and the siphon is often only very pale brown.

94. **C. (Culiciomyia) nebulosus** Theo.

Coast (except Vanga) and highland.

Females. *Biting*—in bush, once only. *Not biting*—in bush, occasional; inside, rare.

Males. In bush and inside, rare.

Larvae. *Outside*—tree holes, not uncommon; bamboo pots, occasional; plant axils, seed pods, coconut-shells, snail-shells, domestic utensils, wells, tanks, pits, swamps and drains, rare. *Inside*—bamboo pots and domestic utensils, rare.

95. **C. (C.) cinereus** Theo.

Coast (Mombasa, Rabai, Gede and Ganda only) and highland (Kaloleni only).

Females. *Biting*—in bush, occasional. *Not biting*—in bush and inside, occasional.

Males. In bush and inside, occasional.

Larvae. *Inside*—latrine, once only.

96. **C. (C.) furlongi** van Someren.

Coast (Mombasa, Rabai, Takaungu and Ganda only) and highland. Not known elsewhere.

Females. *Biting*—in bush, once only. *Not biting*—in bush, scarce.

Males. In bush, rare.

Larvae. Bred material from bamboo pots.

97. **C. (C.) cinerellus** Edw.

Highland (Kwale only). Not known elsewhere in East Africa outside Uganda.

Males. In bush, very rare.

Larvae. *Outside*—streams, rare.

98. **C. (C.) semibrunneus** Edw.

Coast (Mombasa and Gede only). Not known elsewhere in East Africa outside Uganda.

Females. *Not biting*—in bush, very rare.

Males. In bush, very rare.

99. **C. (Mochthogenes) inconspicuosus** (Theo.).

Coast (except Vanga, Takaungu, Ganda and Mambrui) and highland (Kaloleni only).

Females. *Biting*—in bush, rare; on platform, very rare.

Males. In bush, very rare.

Larvae. *Outside*—wells, not uncommon; swamps, drains, streams, pits, pools and rock holes, rare. *Inside*—well, and domestic utensils, rare.

100. **C. (Culex) poicilipes** (Theo.).

Coast (except Msambweni and Takaungu) and highland.

Females. *Biting*—in bush, very rare. *Not biting*—in bush, rare; inside, once only.

Males. In bush, rare; inside, once only.

Larvae. *Outside*—swamps, pools, streams, drains and pits, rare.

101. **C. (C.) bitaeniorhynchus** Giles.

Coast (Malindi only).

Note. Recorded by Edwards (1941).

102. **C. (C.) ethiopicus** Edw.

Coast (Ganda and Mambrui only) and highland.

Females. In bush, once only.

Males. In bush, once only.

Larvae. Bred material from swamps.

Variation. Abdomen of male with apical half of tergites yellow and the female with the apical fourth to one-third yellow or sometimes with large apical lateral triangular yellow patches connected by a narrow yellow band.

103. **C. (C.) annulioris** Theo.

Coast and highland, all localities.

Females. *Biting*—in bush, rare. *Not biting*—in bush, scarce; inside, once only.

Males. In bush, rare.

Larvae. Bred material from swamps.

Variation. Males often and females sometimes with narrow basal yellow bands on all tergites or only on fourth and fifth (females) and apical lateral pale patches often absent on first four tergites and sometimes on all tergites or in the male only indicated by a few pale scales. Pupal trumpets long and narrow and hardly or broadly widened at tip.

Note. As the larvae of *ethiopicus* and *annulioris* are very similar they have not been recorded separately. The group records are as follows:—

Larvae. *Outside*—swamps and streams, not uncommon; wells, scarce; pools, dams and pits, rare.

104. **C. (C.) sitiens** Wied.

Coast and highland, all localities.

Females. *Biting*—in bush, not uncommon; on platform, common. *Not biting*—in bush and inside, not uncommon.

Males. In bush, rare; inside, occasional.

Larvae. *Outside*—wells, not uncommon; swamps, pits and crab-holes, rare.

Variation. White band on proboscis often wider below than above. Fore- and mid-tibiae with the white anterior stripe often indistinct and usually absent on fore-legs. Male terminalia of the Madagascar type (Edwards, 1941). Larvae usually with head setae B and C with 4 and 5 branches respectively. Siphonal index between 3 and 4 and usually one subventral tuft placed proximal to end of pecten.

Note. At Ganda in 1950 there was a large increase in the population of this species and they were abundant biting in the bush and very common biting in the houses but few were caught not biting in the bush and inside. This increase was, at the same time, noticed at Mambrui where it was abundant biting in the bush.

105. **C. (C.) tritaeniorhynchus** Giles.

Coast (except Msambweni).

Females. *Biting*—in bush, occasional. *Not biting*—in bush and inside, occasional.

Males. In bush, very rare; inside, once only.

Larvae. *Outside*—swamps, scarce.

Variation. Proboscis with no pale scales on basal half, pale median ring often hardly extended below. Male palpi with apex narrowly pale (sometimes faintly) and proximal pale ring on shaft may be absent. Larvae with the sub-ventral tufts often bifid and sometimes single and the upper caudal seta has one long and three short branches.

106. **C. (C.) duttoni** Theo.

Coast (except Gede) and highland.

Females. *Biting*—in bush, once only. *Not biting*—in bush and inside, rare.

Males. In bush, rare; inside, once only.

Larvae. *Outside*—swamps, scarce; domestic utensils, wells, pits, pools and dams, rare; water tank in a dhow, once only; tree holes, exceptional. *Inside*—domestic utensils, once only.

107. **C. (C.) argenteopunctatus** ssp. **kingi** (Theo.).

Highland (Kwale only).

Larvae. *Outside*—streams, scarce.

108. **C. (C.) univittatus** Theo.

Coast and highland, all localities.

Females. *Biting*—in bush, occasional. *Not biting*—in bush, scarce; inside, rare.

Males. In bush, scarce; inside, rare.

Larvae. *Outside*—streams and swamps, not uncommon; wells and tanks, occasional; pools, drains, rivers, dams and pits, rare; tree holes and bamboo pots, exceptional.

Variation. Post-spiracular and pre-alar areas often with very few scales and sometimes bare. Tergites often without pale bands and only basal lateral pale spots present. Male often and female sometimes, without a white anterior stripe on hind tibiae.

Note. A few specimens which appear to be var. *neavei* Theo. have been taken. The records are as follows:—

Females. *Biting*—in bush, very rare. *Not biting*—in bush, very rare.

109. **C. (C.) simpsoni** Theo.

Coast (except Takaungu) and highland (Kaloleni only).

Females. *Not biting*—in bush, occasional; inside, rare.

Males. In bush, occasional; inside, rare.

Larvae. *Outside*—swamps, not uncommon; wells, rock holes and pools, occasional; drains, dams, pits, streams and tanks, rare. *Inside*—wells, once only.

Variation. Males and females often with a distinct but broken pale stripe anteriorly on mid-tibiae.

110. **C. (C.) pipiens fatigans** Wied.

Coast and highland, all localities.

FEMALES. *Biting*—in bush, scarce; on platform, rare; inside, not uncommon. *Not biting*—in bush, occasional; inside, abundant.

MALES. In bush, not uncommon; inside, abundant.

LARVAE. *Outside*—wells and tree holes, not uncommon; seed pods, bamboo pots, domestic utensils, tanks, swamps, dams and pits, rare; brackish pools, exceptional. *Inside*—pit latrines and cesspools, common; drains and tanks, not uncommon; gully traps, scarce; domestic utensils, rare.

VARIATION. Abdominal sternites with or without patches of dark scales in the middle. Hind tibiae sometimes without a pale spot at tip or this spot only faintly indicated. Sometimes two lower mesepimeral bristles present on one side of the thorax. Fork of third wing vein 2½–3 times the length of the stem.

111. **C. (C.) antennatus** (Beck.).

Coast and highland, all localities.

FEMALES. *Biting*—in bush, occasional; on platform, very rare. *Not biting*—in bush and inside, rare.

MALES. In bush and inside, rare.

LARVAE. *Outside*—wells, swamps and pools, scarce; tanks, dams, drains and pits, rare; tree holes, exceptional.

VARIATION. Females with small median spots on tergites 4–6 and sometimes on third also; occasionally tergites have basal pale bands which may, but usually do not, meet the lateral patches.

112. **C. (C.) quasiguiarti** (Theo.).

Coast (Ganda and Mambrui only) and highland (Kaloleni only).

FEMALES. *Not biting*—in bush, very rare.

MALES. In bush, very rare.

113. **C. (C.) decens** Theo.

Coast and highland, all localities.

FEMALES. *Not biting*—in bush and inside, rare.

MALES. In bush, rare; inside, once only.

114. **C. (C.) invidiosus** Theo.

Coast (except Msambweni, Kilifi, Gede and Malindi) and highland.

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, not uncommon.

MALES. In bush, not uncommon; inside, once only.

LARVAE. Bred material from swamps.

VARIATION. Scutum often with a narrow marginal band of whitish scales and dorsal scales sometimes light brown. All femora and tibiae white behind except hind tibiae which may be all dark or with a whitish patch in the middle behind; the dark dorsal line on the hind femora may not reach beyond the apical third but often extends to a half. Larvae with head setae C often 3-branched and *e* and *f* with 3–6 and 4–7 branches respectively. Comb a patch of 39–50 scales. Siphonal index about 8, subventral tufts 2–4-branched and the pecten may have as few as 9 teeth. Lateral seta with 2–3 branches.

NOTE. The larvae of *decens* and *invidiosus* are indistinguishable. The group records are as follows:—

LARVAE. *Outside*—wells, not uncommon; streams and swamps, common; pools, rock holes, drains and pits, rare; tree holes, bamboo pots and domestic utensils, exceptional. *Inside*—tanks and bamboo pots, rare.

115. **C. (C.) trifoliatus** Edw.

Coast (Mombasa only) and highland.

FEMALES. *Not biting*—in bush, rare.

MALES. In bush, rare.

VARIATION. Tergites of males with distinct pale basal bands connecting the lateral spots. Hind femora with the whole of the anterior surface dark.

116. **C. (C.) ornatothoracis** Theo.

Coast (Mombasa, Rabai, Ganda and Mambrui only) and highland.

FEMALES. *Not biting*—in bush, rare.

MALES. In bush, rare.

117. **C. (C.) perfuscus** Edw.

Coast (except Vanga) and highland.

FEMALES. *Biting*—in bush, scarce; inside, rare; on platform, once only. *Not biting*—in bush, common; inside, rare.

MALES. In bush, common; inside, rare.

LARVAE. *Outside*—swamps, very rare.

118. **C. (C.) guiarti** Blanch.

Coast (except Vanga, Msambweni and Kilifi) and highland.

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, not uncommon; inside, once only.

MALES. In bush, not uncommon.

LARVAE. *Outside*—swamps, wells and streams, rare.

119. **C. (C.) weschei** ssp. **gediensis** Edw.

Coast (except Vanga and Msambweni) and highlands.

FEMALES. *Biting*—in bush, rare. *Not biting*—in bush, not uncommon.

MALES. In bush, not uncommon.

Larvae. *Outside*—swamps, not uncommon; wells, drains, dams, pools, tanks and domestic utensils, rare.

Variation. Sternites sometimes with dark apical bands.

Note. The larvae of this subspecies ~~is~~ not known for certain but larvae which are indistinguishable from those of *C. weschei* Edw. are found in the area. In addition to the characters given for *weschei* by Hopkins (1952) these larvae have head setae B and C long, bifid, sparsely and finely plumose and the mentum has 5 teeth on either side. The comb consists of 6–8 spines and the siphonal index is about 8. The spines on the dorsal valves of the siphon are long, stout and with 1–2 basal branches and the ventral valves have long hooks. Anal segment with the lateral seta bifid and the upper caudal seta has one long and 1–2 very short branches.

120. **C. (C.) grahami** Theo.

Coast (except Vanga) and highland (Kaloleni only).

Females. *Biting*—in bush, very rare. *Not biting*—in bush, scarce.

Males. In bush, not uncommon.

Larvae. *Outside*—swamps and pools, not uncommon; dams, seepages, drains, pits, wells, tanks and domestic utensils, rare; tree holes and plant axils, exceptional.

Variation. Proboscis often broadly pale below at a half and first few flagellar segments of female antennae with 9–10 hairs in the whorl. Female usually with 2 but sometimes 3 lower mesepimeral bristles but male often with only 1 such bristle. Style of male terminalia not always very broad.

121. **C. (C.) moucheti** Evans.

Coast (except Vanga, Rabai, Takaungu, Ganda and Mambrui).

Larvae. *Outside*—tree holes and fallen leaves, very rare.

Summary.

In this paper a list, with brief notes on prevalence, behaviour and habitat is given of 121 species, sub-species and varieties of mosquitos taken in the last 12 years during field work on the Kenya coast. Two species and one sub-species of the mosquitos found are not yet described. Notes on variation have been included for species that show interesting features in this respect and the distribution of the species in East Africa is also included where it is of interest.

Acknowledgements.

We have to thank the Director of Medical Services, Kenya, for permission to publish this paper.

References.

Bailey, K. P. (1947). A preliminary note on the sylvan mosquitos of Gede.—E. Afr. med. J., **24**, pp. 38–41.

De Meillon, B. (1947). The Anophelini of the Ethiopian geographical region.—Publ. S. Afr. Inst. med. Res., no. 49, 272 pp.

EDWARDS, F. W. (1941). Mosquitoes of the Ethiopian Region. III. Culicine adults and pupae.—499 pp. London, Brit. Mus. (Nat. Hist.).

EVANS, A. M. (1938). Mosquitoes of the Ethiopian Region. II. Anophelini, adults and early stages.—404 pp. London, Brit. Mus. (Nat. Hist.).

GILLETT, J. D. (1946). Notes on the subgenus *Coquillettidia* Dyar (Diptera, Culicidae).—Bull. ent. Res., **36,** pp. 425–438.

GILLETT, J. D. (1949). Further notes on the Ethiopian species of *Taeniorhynchus* Arribalzaga (Diptera, Culicidae).—Proc. R. ent. Soc. Lond., (B) **18,** pp. 97–102.

HADDOW, A. J. (1946). The mosquitoes of Bwamba County, Uganda. IV. Studies on the genus *Eretmapodites*, Theobald.—Bull. ent. Res., **37,** pp. 57–82.

HADDOW, A. J., VAN SOMEREN, E. C. C., LUMSDEN, W. H. R., HARPER, J. O. & GILLETT, J. D. (1951). The mosquitoes of Bwamba County, Uganda. VIII. Records of occurrence, behaviour and habitat.—Bull. ent. Res., **42,** pp. 207–238.

HAMON, J. (1953). Une nouvelle espèce d'*Aedes* de l'île de la Réunion (Diptère Culicidae).—Nat. Malgache, **5,** pp. 35–41.

HARRIS, W. V. (1942). Notes on Culicine mosquitos in Tanganyika Territory.—Bull. ent. Res., **33,** pp. 181–193.

HOOGSTRAAL, H. & KNIGHT, K. L. (1951). Observations on *Eretmapodites silvestris conchobius* Edwards (Culicidae) in the Anglo-Egyptian Sudan.—Amer. J. trop. Med., **31,** pp. 659–664.

HOPKINS, G. H. E. (1952). The mosquitoes of the Ethiopian Region. I. Larval bionomics of mosquitoes and taxonomy of Culicine larvae.—2nd edn., 355 pp. London, Brit. Mus. (Nat. Hist.).

KNIGHT, K. L. & CHAMBERLAIN, R. W. (1948). A new nomenclature for the chaetotaxy of the mosquito pupa, based on a comparative study of the genera (Diptera: Culicidae).—Proc. helminth. Soc. Wash., **15,** pp. 1–10.

LEWIS, D. J. (1944). A new subspecies of *Aëdes leesoni* Edwards (Dipt., Culicidae) from the Sudan.—Proc. R. ent. Soc. Lond., (B) **13,** pp. 27–29.

MATTINGLY, P. F. (1953). The sub-genus *Stegomyia* (Diptera: Culicidae) in the Ethiopian Region. II. Distribution of species confined to the East and South African sub-regions.—Bull. Brit. Mus. (Nat. Hist.), Ent., **3,** pp. 1–65.

VAN SOMEREN, E. C. C. (1946*a*). Ethiopian Culicidae: notes and descriptions of some new species and hitherto unknown larvae and pupae (Diptera).—Trans. R. ent. Soc. Lond., **96,** pp. 109–124.

VAN SOMEREN, E. C. C. (1946*b*). Ethiopian Culicidae. Tribe Megarhinini—notes and descriptions.—Trans. R. ent. Soc. Lond., **97,** pp. 177–186.

VAN SOMEREN, E. C. C. (1946*c*). Ethiopian Culicidae—descriptions of the adults and pupae of two new species and two subspecies of the genus *Aëdes* from East Africa (Diptera).—Proc. R. ent. Soc. Lond., (B) **15,** pp. 1–6.

VAN SOMEREN, E. C. C. (1947). Ethiopian Culicidae—notes and descriptions.—Proc. R. ent. Soc. Lond., (B) **16,** pp. 129–132.

van Someren, E. C. C. (1949). Ethiopian Culicidae—*Eretmapodites* Theobald: description of four new species of the *chrysogaster* group with notes on the five known species of this group.—Proc. R. ent. Soc. Lond., (B) **18,** pp. 119–129.

van Someren, E. C. C. (1950*a*). Ethiopian Culicidae: description of a new *Aëdes* from East Africa and notes on two known *Aëdes* with which it might be confused.—Proc. R. ent. Soc. Lond., (B) **19,** pp. 7–10.

van Someren, E. C. C. (1950*b*). Ethiopian Culicidae: a description of a new sub-species of *Aëdes* (*Aëdimorphus*) *tricholabis* Edwards.—Proc. R. ent. Soc. Lond., (B) **19,** pp. 67–69.

van Someren, E. C. C. (1951). New Culicini from Kenya and Uganda.—Proc. R. ent. Soc. Lond., (B) **20,** pp. 1–9.

van Someren, E. C. C. (1954). New Culicini from the Kenya Coast.—Proc. R. ent. Soc. Lond., (B) **23,** pp. 103–109.

Wiseman, R. H., Symes, C. B., McMahon, J. C. & Teesdale, C. (1939). Report on a Malaria Survey of Mombasa.—60 pp. Nairobi, Govt. Printer.

THE TRANSMISSION OF BANCROFTIAL FILARIASIS ON UKARA ISLAND, TANGANYIKA.

III.—BITING-INCIDENCES ON MAN AND FILARIAL INFECTIONS IN WILD-CAUGHT MOSQUITOS.

By A. Smith, Ph.D.
Entomologist, Filariasis Research Unit, Mwanza, Tanganyika.

A description of Ukara Island has been given in a previous paper (Smith, 1955*a*). Some parts of the island have low and others a higher incidence of bancroftial microfilaraemia (Smith, 1955*b*). The determination of vectors of human filariasis in the field depends on circumstantial evidence, and Smith (1955*b*) considers first the general coincidence in distribution of high hut-infestations and proximity of breeding places of *Anopheles gambiae* Giles and *A. funestus* Giles with high incidences of bancroftial microfilaraemia in villages of Ukara. In the present paper the writer records the biting-incidences of mosquitos on man and discusses the circumstances in which he is bitten by different species under conditions on Ukara. The paper goes on to describe the evidence obtained of filarial infections in wild-caught mosquitos.

Seasonal Biting-incidences on Man seated inside and outside Huts at Night.

The Bakara usually come home from cultivating their fields towards dusk (approx. 7 p.m. East African Standard Time). They sit outside their huts if it is a starlight or moonlight night and warm. Sometimes there is a small fire to sit round, built of weeds that have been taken from fields during the day. The main meal of the day is prepared in the hut at about 9 p.m. E.A.T. and is eaten usually just inside the doorway. If it is a fine night and there is a fire outdoors, or moonlight, then the meal may be taken outdoors. After the meal, doors are closed and the people retire to bed until dawn (approx. 6 a.m. E.A.T.).

The inhabitants are bitten by mosquitos at night, sometimes so frequently that they are unable to sleep. By catching mosquitos biting a man in a hut at night, data was obtained on species biting man in huts and their abundance. The seasonal incidence of these species biting man in huts is found by catches on human " bait " during the short dry season (January and February), the long rains (March–May), the long dry season (June–October) and the short rains (November and December). People are bitten outdoors during the short period spent near their huts in the evening. By catching mosquitos on a man outdoors, simultaneously with catches indoors, it was possible to distinguish between largely endophilic and exophilic species which bite man and to record their relative abundance. The technique was that a mosquito catcher and human bait sat close to the main bed in a hut and a similar pair was placed several yards away from the hut. A typical hut was selected in each of two villages, Nyamanga and Bubanja, and catches were made for three nights in each village from 7 p.m. to 3 a.m. The mosquitos were caught in 6″ × ½″ test-tubes with the aid of a torch. The writer identified the material at hourly intervals and supervised collections. Nyamanga and Bubanja are widely separated. Nyamanga, with 25 per cent. of the people infected, is situated high up near the centre of the island (Smith, 1955*b*, p. 441) and Bubanja, with a 26 per cent. incidence of infection, lies on the north coast near a swamp.

TABLE I.

Catches on human bait at different seasons. Each figure is the total number of mosquitos caught in three nights between 7 p.m. and 3 a.m.

Species	Short dry season (January and February) catches between 19th February and 18th March				Long rains (March, April and May) catches between 27th May and 6th June				Long dry season (June–October)					Short rains (November and December) catches between 22nd December and 2nd January			
									Catches July 13 –17th	Catches between 23rd September and 3rd October							
	Nyamanga		Bubanja		Nyamanga		Bubanja		Bubanja	Nyamanga		Bubanja		Nyamanga		Bubanja	
	In doors	Out-doors	In-doors	Out-doors	In-doors	Out-doors	In-doors	Out-doors	In-doors	In-doors	Out-doors	In-doors	Out-doors	In-doors	Out-doors	In-doors	Out-doors
A. gambiae Giles	89	30	76	24	471	159	648	62	271	0	0	8	0	0	0	44	3
A. funestus Giles	69	22	20	3	32	18	85	4	141	0	0	3	0	1	0	8	0
A. coustani Lav.	0	0	0	2	1	8	2	74	2	0	0	0	3	0	0	0	1
A. rufipes (Gough)	0	0	0	0	1	3	0	1	0	0	0	0	0	0	1	0	0
A. squamosus Theo.	0	0	0	0	0	3	0	3	—	—	—	—	—	—	—	—	—
A. pharoensis Theo.	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	12	0
A. maculipalpis Giles	0	0	0	0	0	0	0	1	—	—	—	—	—	—	—	—	—
A. wellcomei Theo.	0	0	0	0	0	0	0	1	—	—	—	—	—	—	—	—	—
Aë. africanus (Theo.)..	0	42	0	1	0	19	0	1	0	0	0	0	1	0	0	0	0
Aë. vittatus (Big.)	0	0	0	0	0	1	0	0	—	—	—	—	—	—	—	—	—
C. univittatus Theo.	0	0	0	4	0	2	0	1	5	0	0	0	0	0	0	9	18
C. antennatus (Beck.)	0	2	1	59	0	0	2	26	0	0	0	1	3	0	1	0	0
C. annulioris Theo.	0	8	3	20	6	40	15	73	15	0	0	0	1	0	2	0	1
T. africanus (Theo.)	1	10	5	54	0	5	6	38	17	0	1	30	68	0	4	21	123
T. uniformis (Theo.)	1	14	3	95	0	2	9	194	16	0	0	9	36	0	1	7	44

Occasional individuals of many species of mosquito bite man at night (Table I). Indoors, by far the commonest biting species are *A. gambiae* and *A. funestus*, with smaller numbers of *Culex annulioris* Theo., *Taeniorhynchus africanus* (Theo.) and *T. uniformis* (Theo.). Common species outdoors are *A. gambiae* and *A. funestus* and exophilic *A. coustani* Lav. (type form not separated from var. *ziemanni* Grünb.), *C. annulioris*, *C. antennatus* (Beck.), *T. africanus*, *T. uniformis* and *Aëdes africanus* (Theo.) with small numbers of *C. univittatus* Theo.

The seasonal collections shown in Table I were made during 1952, which was unusual in respect to rainfall; the short rains failed and this is reflected in the low incidences of *Anopheles gambiae* and *A. funestus* in December. *A. pharoensis* Theo., a rare mosquito at most times, unaccountably became more common at Bubanja towards the end of the drought. It has been shown in an earlier paper that a rise and fall in lake level occurs, which aids irrigation in certain coastal areas of the island (Smith, 1955*b*). The effect of this rise and fall on the seasonal incidences of *A. gambiae* and *A. funestus* is small because most of their breeding grounds are in river valleys irrigated by rain falling on the island. Rainfall and lake-level measurements for 1952 are given in Table II with the indoor biting-incidences of *A. gambiae* and *A. funestus* at Bubanja on the coast. The lake level rises to 84 cm. above zero in June and then declines. The incidence of *A. gambiae* and *A. funestus* follows rainfall incidence so that a peak of *A. gambiae* occurs shortly after the long rains in April and a peak of *A. funestus* in July (Table II) when breeding conditions have become optimum.

A. gambiae, *A. funestus* and *C. annulioris* are the only species common in both villages: *T. africanus*, *T. uniformis* and *C. antennatus* are largely found at Bubanja, and *Aë. africanus* at Nyamanga. The biting-habits of *A. gambiae* and *A. funestus* make them suspect as principal vectors of bancroftial filariasis for they are the only species which bite man chiefly indoors at night and are common in both villages.

TABLE II.

Data showing that incidences of *A. gambiae* and *A. funestus* depend more on the amount of rain falling on the island than on changes in lake level.

1952 Month	Ukara rainfall in inches	Lake level, cm. above zero	No. collected indoors at Bubanja for 3 nights between 7 p.m. and 3 a.m.	
			A. gambiae	*A. funestus*
January .. February ..	1·74 4·95	40 40	76	20
April .. May	17·61 12·34	62 75	648	85
June .. July	0·10 1·00	84 80	271	141
August .. September ..	0·98 4·75	65 57	8	3
November .. December ..	1·64 0·10	49 50	44	8

The Exposure to Mosquitos of People sleeping in their Huts.

By examining the type and amount of covering of people sleeping in their huts, it is possible to form some idea of the extent to which the occupants are exposed to attack by mosquitos. The following account is based on an examination of sleeping conditions in forty huts. In most cases, adults share a blanket which, when new, is impenetrable by mosquitos. Most blankets seen were threadbare and the occupants said mosquitos bit through them. During their first few years, children sleep with the father and mother and the mother protects the child against bites by covering it with the blanket. In cases where there are two or three very young children the youngest sleeps with the mother and the oldest with the father on a separate bed. Depending on the number of children in the family, a child usually leaves the main bed between four and eight years old. There is a sharp contrast between the protection of the child from mosquitos when it is in the main bed and when in the children's bed. Children in the second bed are usually scantily covered in pieces of cotton cloth, in some cases there is no clothing. Mosquitos can bite through the cotton cloth (Americani) easily. The period during which Bakara are most exposed to bites is between six and sixteen years old. At sixteen years old a man can build a separate hut and is eligible for marriage by Ukara custom and by Catholic law. A woman is eligible at twelve years by Ukara custom and fourteen years by Catholic law which affects less than a quarter of the island's inhabitants. At sixteen years a man buys a blanket, and by the same age a woman is usually married and sharing one.

Day-biting Mosquitos.

Outdoors.

The inhabitants are bitten by several species of mosquito during the daytime. Chief of these are species of *Aëdes.*

Villages are situated in the shelter of trees which protect huts from devastation by occasional severe winds and storms. Most of the trees have been planted by the people and they are usually pollarded and constantly pruned. Leaves are used for daily cattle fodder and suckers and branches for building houses and domestic furnishings. Small plantations of trees pollarded close to the ground are frequently the site of latrines. Other sites used as latrines are amongst naturally occurring rocks screened by bushes and pollards. These pollards and rocks are natural resting places of *Aë. africanus*, *Aë. apicoargenteus* (Theo.), *Aë. aegypti* (L.) and *Aë. vittatus* (Big.), and anyone cutting branches or leaves for cattle fodder from these pollards between dawn and dusk is liable to be bitten by these species. The latrines are mostly visited for defecation in the evening or at night. Visits are made chiefly at night after the main meal of the day which is at approx. 9 p.m. E.A.S.T. It is believed by the Bakara that should their faeces fall into the hands of a witch doctor (there are many on the island) he will be able to exert some influence on them; hence they take the precaution of concealing their identity by visiting the latrines at night. Urine is considered a valuable addition in making compost and is passed on the compost in the cattle section of their huts. Latrines are resting places for many species of mosquitos. At Bubanja village, people are occasionally bitten by *Taeniorhynchus africanus* and *T. uniformis* during day-time visits to cut branches and leaves, and more frequently by these species when they visit the latrines for defecation at night. But the habits of the people expose them to day-biting mosquitos for only short periods. Villages are almost entirely vacated during day-time, for men and women spend most of the day in their fields and the children take cattle out to pasture among the hills. The possibility of a day-time vector, however, exists because it is known that the microfilarial level of *Wuchereria bancrofti* in the peripheral blood of man, although periodic with a high peak at night, does not drop to zero during the day-time (Laurie, 1950).

The following numbers of mosquitos were caught on five people sitting near bushes and trees at Nyamanga village between 7.30 a.m. and 7.30 p.m. during one day in May: *Aë. africanus* 91, *Aë. apicoargenteus* 77, *Aë. aegypti* 8, *Aë. vittatus* 1, *T. uniformis* 3 and *C. univittatus* 6. In another collection outdoors in the same village, in April, the following numbers were collected on four people between 9 a.m. and 7 p.m.: *Aë. africanus* 94, *Aë. apicoargenteus* 72, *Aë. aegypti* 6, *Aë. vittatus* 4, *C. univittatus* 10, *C. annulioris* 2, *A. coustani* 2 and *A. funestus* 1. It can be seen that *Aë. africanus* and *Aë. apicoargenteus* are the commonest species which bite man outdoors by day. In collections made at night between 7 p.m. and 3 a.m. *Aë. apicoargenteus* was absent, its biting-activities apparently being inhibited by darkness and *Aë. africanus* was taken in greater numbers at Nyamanga between 7 and 8 p.m. Of the mosquitos which bite man outdoors chiefly during the day-time, only *Aë. africanus* and *Aë. apicoargenteus* bite in numbers large enough to be considered as possible vectors.

Indoors.

There is a low level of biting-activity on man by *A. gambiae* and *A. funestus* in huts during day-time in April, so that a small amount of day-time transmission by these species might occur. An indication of a difference in biting-activity between the two species in day-time is given in catches on a man in a cone hut (Table III). It can be seen from the Table that greater numbers of *A. gambiae* bite during the night than during the day but in *A. funestus* the difference is not so great. The explanation offered is that biting in *A. funestus* is partly inhibited at night by the odour of cattle which makes detection of man difficult. When the door is open by day the odour of cattle is dispersed from the hut.

TABLE III.

Catches of *A. gambiae* and *A. funestus* off man in a cone hut, indicating that the biting-activity of *A. funestus* is more inhibited at night than that of *A. gambiae*.

		Time												Total
		8	9	10	11	12	1	2	3	4	5	6	7	
A. gambiae ..	Night	8	19	22	15	23	26	19	35	13	30	16	10	236
	Day	5	5	4	3	0	0	0	0	1	1	1	3	23
A. funestus ..	Night	0	3	5	2	2	4	3	4	0	1	0	1	25
	Day	0	3	2	1	0	0	0	1	1	0	3	4	15

Filarial Infections in Wild-caught Mosquitos on Ukara.

Although the relationships of densities, distribution and of biting-habits of *A. gambiae* and of *A. funestus* to the incidence of bancroftial filariasis in different villages indicates that one, or both species are probably vectors of the human infection, further evidence to determine the vectors of the disease was derived from examinations of wild-caught mosquitos of numerous species for developing filarial larvae. Mosquitos for dissection were collected from the villages Nyamanga and Bubanja. Almost all *A. gambiae*, *A. funestus* and *A. pharoensis* were collected resting on the walls inside huts and most specimens of other species off human bait outdoors. Although *A. funestus* and *A. rivulorum* breed together in a coastal swamp at Bubanja, only *A. funestus* appears to rest in huts. Egg batches obtained from 26 mosquitos of the *funestus* group, captured in huts at Bubanja, were all *A. funestus*. Dissected mosquitos were examined by the writer or a trained African and all positives classified by the writer. A mosquito was examined by preparing two slides; one of the head and thorax and the other of the abdomen. The following developmental stages were recognised:—

1. *Early developmental forms* resembling exsheathed microfilariae but present in thoracic muscles and quiescent.
2. *Sausage forms.* Short, thick and slightly flexed, giving a sausage-like appearance, with highly granular cytoplasm. Quiescent.
3. *Late developmental forms.* Up to three times as long as sausage forms. Thinner and quiescent.
4. *Preinfective forms.* Thread-like and sluggishly mobile.
5. *Infective forms.* Longer, thinner and with cytoplasm clearer than in preinfective forms. Active.

Stages 1–3 occur in the thorax, stage 4 in the thorax and head and stage 5 in the head and proboscis. Table IV summarises the results, and details of all infected mosquitos are given in the Appendix.

TABLE IV.

Summary of results of the dissections.

Species	No. dissected	No. infected	No. infective
A. gambiae	3,287	65 (2%)	19 (0·6%)
A. funestus	1,228	39 (3%)	13 (1%)
A. pharoensis ..	93	12 (13%)	0
A. coustani	105	0	0
Aë. africanus ..	404	0	0
Aë. apicoargenteus ..	149	0	0
Aë. aegypti	9	0	0
Aë. vittatus	11	0	0
C. annulioris ..	262	0	0
C. antennatus ..	34	1	0
T. africanus	1,106	8	0
T. uniformis ..	1,080	6	0

Points which emerge from the results are:—

(a) Among the species dissected (see Table IV), infective filarial forms were found only in *A. gambiae* and *A. funestus*. The percentage with infective forms is low, averaging 0·6 per cent. for *A. gambiae* and 1·0 per cent. for *A. funestus*. Although there may be as many as eight infective forms in one mosquito (*A. funestus*), there are usually only one or two present.

(b) Infections in *A. gambiae* and *A. funestus* are heavier near the beginning of the long dry season (June–October) than in the long wet season (March–May). Of 748 *A. gambiae* dissected in July 1952, 19 (2·5%) were infected and of 100 dissected at the end of July 1953, 13 per cent. were infected, whereas in April 1952 of 776 dissected 6 (0·8%) were infected. Of 493 *A. funestus* dissected in July, 16 (3·3%) were infected compared with 10 (0·3%) infected of 358 dissected between March and May. Reduction of breeding grounds of *A. gambiae*, which occurs at the onset of the long dry season and the lower temperature at the beginning of it, might give rise to an increase in average age of the adult *gambiae* population in July. This would increase the probability of infected specimens being taken in collections. The increase in the infection rate of *A. funestus* in July, when *funestus* is at its peak incidence, is more likely to be related to direct effects of climate on the life-span of the adult mosquito and/or the effects of climate on the filarial development in the mosquito.

(c) Immature filarial infections occur in *A. pharoensis*, *T. africanus*, *T. uniformis* and *C. antennatus*. Heavy infections with thoracic forms, but no head or proboscis infections, occur in *A. pharoensis*. Development may not reach completion, or more likely, in view of its sudden appearance in numbers followed by abrupt and virtual disappearance, the adult *pharoensis* may not live long enough for filarial development to reach completion. Filarial worms die at an early stage in *T. africanus* and *T. uniformis*.

(d) Early stages of development are not usually found together with preinfective and infective forms. Also the average number of early developmental forms in infected *A. gambiae* and *A. funestus* is lower than in other species of mosquito, in which filarial development does not reach completion. The averages are: *A. gambiae* 2·9, *A. funestus* 3·2, *T. africanus* 4·0, *T. uniformis* 13·0 and *A. pharoensis* 6·5.

No nematode infections of the abdomen were seen in mosquitos dissected, with the exception of a single active filaria in one *A. funestus* and one *A. gambiae*. Posterior development in the Malpighian tubules was searched for in all specimens, but none was found.

Records kept of numbers of microfilariae in the stomach blood of *A. gambiae* and *A. funestus*, collected from huts and dissected the same day, show that the average count is 3 microfilariae between limits 1 and 12 for 65 *A. gambiae* with microfilariae, and 2–4 microfilariae between limits 1 and 15 for 12 *A. funestus*.

Evidence, derived from the examination of wild-caught mosquitos for developing filarial larvae, therefore, confirms findings, based on the relationships of densities, distribution and biting habits of *A. gambiae* and *A. funestus*, that these two species are almost, if not entirely, responsible for the transmission of bancroftial filariasis on Ukara Island.

Summary.

The seasonal biting-incidences on man of several species of mosquito inside and outside huts of villages on Ukara Island, Tanganyika, between 7 p.m. and 3 a.m. East African Standard Time are recorded. *Anopheles gambiae* Giles and *A. funestus* Giles were by far the most common indoor biters in both of the villages which received study: they were also taken biting outdoors in fair numbers. *Taeniorhynchus africanus* (Theo.) and *T. uniformis* (Theo.) were common outdoor biters in a village near a swamp, but were taken in only small numbers off human " bait " in a cone hut.

A study of sleeping arrangements in huts showed that people between six and sixteen years of age were most exposed to the risk of mosquito bites at night, since they were least protected by covers and clothing.

The inhabitants were bitten by *Aëdes africanus* (Theo.) and *Aë. apicoargenteus* (Theo.) outdoors by day, and by small numbers of *A. gambiae* and *A. funestus* in huts during daylight hours in April.

The results are given in detail of dissections for developing filarial worms in over seven thousand mosquitos. Proboscis infections occurred in *A. gambiae* and *A. funestus*. Immature (thoracic) forms were found in *A. pharoensis* Theo., *T. africanus*, *T. uniformis* and *Culex antennatus* (Beck.).

It is concluded that the biting-habits of *A. gambiae* and *A. funestus* point to them as more likely vectors of bancroftial filariasis than other species with developing filarial worms.

Acknowledgements.

I am indebted to Mr. Francisco Balole for his help in microscopy and Mr. Wilson Ngashi, Mr. Paulo Nzumbi and Mr. Amos Ndalo for their faithful services in collecting mosquitos.

References.

East Africa High Commission [1951]. Filariasis Research Unit. Annual report 1950.—61 pp. Nairobi.

Smith, A. (1955*a*). The transmission of bancroftial filariasis on Ukara Island, Tanganyika. I. A geographical and ecological description of the island with an annotated list of mosquitos and other arthropods of medical importance.—Bull. ent. Res., **46,** pp. 419–436.

Smith, A. (1955*b*). The transmission of bancroftial filariasis on Ukara Island, Tanganyika. II. The distribution of bancroftial microfilaraemia compared with the distribution of hut-haunting mosquitos and their breeding places.—Bull. ent. Res., **46,** pp. 437–444.

APPENDIX.

Details of infected mosquitos.

The site of the pre-infective and infective worms is indicated by:
T = thorax
H = head
P = proboscis
F = free on slide.

	A. gambiae							*A. funestus*						
1952 Month	No. dissected	Specimen No.	Early dev. forms	Sausage forms	Late dev. forms	Preinfective forms	Infective forms	No. dissected	Specimen No.	Early dev. forms	Sausage forms	Late dev. forms	Preinfective forms	Infective forms
February	65	1	4					26						
		2	2											
March	731	3	1					169	1				4	6H
		4				1T	1H		2				2	1P
		5				1T			3				8T	2P3H
		6		2					4					2P6H
April	776	7		6				125						
		8	6											
		9		6										
		10	4											
		11				2H	1H							
		12				3H	2P							
May	160							64	5		1			
									6			2		1F
									7	4				
									8	2				
									9			3		
									10	2				

APPENDIX—*cont.*

	A. gambiae							*A. funestus*						
1952 Month	No. dissected	Specimen No.	Early dev. forms	Sausage forms	Late dev. forms	Preinfective forms	Infective forms	No. dissected	Specimen No.	Early dev. forms	Sausage forms	Late dev. forms	Preinfective forms	Infective forms
June		13	1						11			2		
		14	4						12	6				
		15	4						13	6				
	503	16				1	1	189	14		2			
		17			12				15		1			
		18					2F1H							
		19				3								
		20	1											
		21	7											
		22	3											
		23					1F							
		24	4											
		25					1F							
		26				4T								
		27	4											
		28	4											
July		29	2						16	1				
		30	4						17					1F
		31	1						18	3				
		32		2					19	1				1F
		33	1				3F		20			1		
		34					2F		21				2	
		35			1				22		2			
		36	1						23		6			
		37		2					24					2H
	748	38	3					493	25			4		
		39	2						26					1F
		40	1						27	2				
		41					1H		28					1F
		42		2					29			1		
		43		1					30	3				
		44			4				31		2			
		45					1F		32					1F
		46			1									
		47					1H							
October		48	4						33	3				
	55	49	5					36	34		1			
									35			2		
1953 January		50					1H							
	149	51					1F							
		52					1F							
July		53		1					36	1				
		54		2				100	37				2	1
		55	1						38	1				
		56		3					39					1
		57				4H	1P							
		58	1	1										
		59					1F							
	100	60					1							
		61		1		1								
		62			1									
		63		4										
		64				1F								
		65					1F							

Appendix—*cont.*

	T. africanus							*A. pharoensis*						
	No. dissected	Specimen No.	Early dev. forms	Sausage forms	Late dev. forms	Preinfective forms	Infective forms	No. dissected	Specimen No.	Early dev. forms	Sausage forms	Late dev. forms	Preinfective forms	Infective forms
	1,106	1		19				93	1	7				
		2	7						2		2			
		3	4						3	6				
		4	3						4	18				
		5	1						5	2				
		6	2						6			2		
		7		1					7			2		
		8	7						8	1	2			
									9	4				
									10	11	3			
									11	3	7			
									12		2			
	T. uniformis							*C. antennatus*						
	1,080	1	43					34	1	1				
		2	23											
		3	7											
		4	1											
		5	4											
		6	1											

ON THE TRANSMISSION OF BANCROFTIAL FILARIASIS ON UKARA ISLAND, TANGANYIKA.

IV.—HOST-PREFERENCES OF MOSQUITOS AND THE INCRIMINATION OF *ANOPHELES GAMBIAE* GILES AND *A. FUNESTUS* GILES AS VECTORS OF BANCROFTIAL FILARIASIS.

By A. Smith, Ph.D.
Entomologist, Filariasis Research Unit, Mwanza, Tanganyika.

This paper is one of a series on the transmission of bancroftial filariasis of man on Ukara Island, Tanganyika. The reader is referred to an earlier paper (Smith, 1955*a*) for a geographical and ecological description of the island, and to Smith (1955*b*, 1955*c*) for preliminary observations on the distribution of filariasis in the villages and animals on the island and the distribution and habits of potential vectors of the human infection. It is shown (Smith, 1955*b*) that *Anopheles gambiae* Giles and *A. funestus* Giles form over 90 per cent. of the hut-resting mosquito population and that there is a general coincidence in distribution between high hut-densities of these species and high microfilaraemia rates among people in different villages. Also that villages with high incidences of bancroftial filariasis are near extensive breeding grounds of these species. In Smith (1955*c*) it is also shown that the inhabitants are bitten by *Aëdes apicoargenteus* (Theo.) and *Aë. africanus* (Theo.) during daylight hours, and by *Aë. africanus*, *Taeniorhynchus africanus* (Theo.) and *T. uniformis* (Theo.) as well as small numbers of other species, outdoors in the evenings. These species rarely or uncommonly bite man inside huts, but he is bitten at night by large numbers of *A. gambiae* and *A. funestus*, and it is shown that, among mosquitos which bite man, infective filarial forms have been found only in *A. gambiae* and *A. funestus*, although infections with immature worms occur in *A. pharoensis* Theo., *T. africanus*, *T. uniformis* and *Culex antennatus* (Beck.). One cannot deduce, with certainty, the definitive host of a filarial worm by morphological examination of infective or developmental forms in a mosquito in an area, such as Ukara, where filarial infections occur in wild and domestic animals as well as in man. The present paper is concerned, therefore, with the extent to which different species of mosquitos feed on man, domestic and wild animals under Ukara conditions. This information is of much importance in assessing what species of mosquitos are vectors of the human filarial infection. Outdoor resting places are described as part of this study. The paper concludes with a discussion on the habits of different mosquitos and on the incrimination of the principal vectors of bancroftial filariasis. Suggestions are made as to the vectors of the other filarial infections which occur in animals on the island.

Host-preferences of Mosquitos resting in Huts.

The traditional hut is cone-shaped and consists of a framework of sticks thatched from top to bottom. Huts in all villages are mainly of this type. A survey of forty cone huts in different parts of the island shows that their average height is 20 ft. 10 in. and their diameter at the base 22 ft. 8 in. The average number of occupants is 3·3 Africans, 2·8 cattle and 1·6 goats. An incomplete screen divides a hut into rough halves, one occupied by Africans and the other by cattle and goats. A perch for domestic fowl usually stands above the pit occupied by cattle. Dogs are uncommon, there being no more than four or five in a large village. The selection of hosts by mosquitos found resting in huts has been investigated by precipitin tests and by observations for nucleated erythrocytes in gorged specimens, and by direct catches of mosquitos alighting on man and domestic animals in huts. The results of these different methods of investigation are set out below.

Precipitin tests.

As almost the entire mosquito population resting in huts consists of *A. gambiae* and *A. funestus*, many blood-smears of these species could be prepared in a short time, but smears of other hut-haunting species could only be obtained by collecting throughout several months. The results are summarised in Table I, which shows that man and ox are the chief sources of blood of hut-resting mosquitos. *A. gambiae* and *A. funestus* feed almost entirely on man. *A. pharoensis* feeds more on man than on ox, whereas the Culicines feed more on ox than man. *Culex annulioris* Theo., next in abundance to *A. funestus* in huts, feeds largely on ox. In another series of precipitin tests (the results of some of which have already been published by Smith, 1955*a*), 199 (92%) of 217 blood-feeds of *A. gambiae* examined for man, ox, goat and dog were positive for man, 12 (6%) for ox and none for goat or dog: two specimens had fed on both man and ox. Of 96 blood-feeds of *A. funestus*, 77 (80%) were positive for man and none for ox, goat or dog. Smaller numbers of other species were examined. Of 31 *T. africanus*, 12 were positive for man, 13 for ox and none for goat, dog or fowl: one had fed on both man and ox. Of 24 *A. pharoensis*, ten fed on man, four on ox and none on goat, dog or fowl. Of 23 *T. uniformis*, nine fed on man, 11 on ox, one on dog, one on fowl and none on goat. Of 60 *C. annulioris*, six fed on man, 40 on ox, one on man and ox, and one on ox and goat: none fed on dog or fowl. Of nine *C. univittatus* Theo., four fed on man and five on ox. It thus appears that goats, dogs and domestic fowl form an insignificant part in the diet of blood-fed mosquitos resting in huts.

TABLE I.

The percentage of blood-fed mosquitos in huts which feed on man and ox.

Species	No. tested	Man		Ox		Negative for man & ox	
		No.	%	No.	%	No.	%
A. gambiae Giles ..	216	197	91	not	tested	19	9
A. funestus Giles ..	169	143	85	not	tested	26	15
A. pharoensis Theo.	33	16	48	7	21	10	31
C. annulioris Theo.	147	12	8	114	78	21	14
C. univittatus Theo.	52	7	14	35	67	10	19
T. africanus (Theo.)	52	14	27	25	48	13	25
T. uniformis (Theo.)	36	10	28	22	61	4	11

Precipitin tests on separate collections of *A. gambiae* and *A. funestus* from the halves of the huts occupied by Africans (a), and cattle (b), respectively, indicate that *A. gambiae* feeds more readily on ox than *A. funestus* under the conditions in an Ukara cone hut in which human beings and cattle are housed together. Of 236 *A. gambiae* tested from (a), 223 (95%) fed on man and four (1·7%) on ox; and of 196 tested from (b), 148 (76%) fed on man and 24 (12%) on ox. Of 243 *A. funestus* from (a), 185 (76%) fed on man and three (1·2%) on ox; and of 90 from (b), 62 (69%) fed on man and one (1·1%) on ox. In order to get sufficient specimens of *A. funestus*, it was necessary to make use of a number of blood meals in rather advanced stages of digestion and this accounts for the low number of positives. An important difference between *A. gambiae* and *A. funestus* in these tests is that less than 2 per cent. of *A. funestus* in the halves of the huts occupied by man or cattle fed on ox, whereas, although less than 2 per cent. of *A. gambiae* in the halves occupied by man fed on ox, 12 per cent. in those occupied by cattle were positive for ox.

Hand-catches off man, cow and goat in huts.

The experiment took place in a cone hut occupied by two adults, one child, three cows and three goats, one catcher being assigned to collecting from each type of host. A catcher sat near his bait and, with the aid of a torch, caught mosquitos in test-tubes as they alighted. The catchers rotated each night of the nine days' experiment. The catches extended from 10 p.m. to 4 a.m. and mosquitos were examined at hourly intervals. The first and last three days of the experiment were supervised by the writer and the other three days by the chief African assistant. The door was closed except for entry and exit of the supervisor at hourly intervals. The experiment took place between 23rd June and 2nd July and the results are summarised in Table II.

TABLE II.

The number of mosquitos caught off man, cow and goat in a cone hut in nine nights.

Species	Total caught	Man		Cow		Goat	
		No.	%	No.	%	No.	%
A. gambiae Giles ..	236	178	75	23	10	35	15
A. funestus Giles ..	84	74	88	3	4	7	8
C. annulioris Theo. ..	149	20	13	77	52	52	35
C. univittatus Theo. ..	19	4	21	8	42	7	37
A. longipalpis (Theo.) ..	3	0	—	2	—	1	—
T. uniformis (Theo.) ..	5	3	—	0	—	2	—
T. africanus (Theo.) ..	9	4	—	2	—	3	—

The results show that 75 per cent. of *A. gambiae*, 88 per cent. of *A. funestus*, 13 per cent. of *C. annulioris* and 21 per cent. of *C. univittatus* were caught off man, thus confirming the results of precipitin tests which show that man is a more important host to *A. gambiae* and *A. funestus* than to hut-haunting Culicines, and that *A. funestus* is probably more anthropophilic than *A. gambiae*. Hand-catches off domestic animals are probably affected by the nearness of the catchers who might attract more anthropophilic mosquitos on to the animals than occurs under natural conditions. This effect would partly explain the 15 per cent. *A. gambiae* and 8 per cent. *A. funestus* caught on goat. A further tendency to randomisation in host choice as observed by hand-catching techniques may be because catches of mosquitos alighting on a host do not give as critical a distinction between host preferences as collections of blood-fed mosquitos. The latter have completed the whole series of responses leading to taking a blood-meal, whereas a mosquito alighting on a host may find it unsuitable and fly away unfed under natural conditions.

Examination of mosquito blood-meals for nucleated corpuscles.

Freshly dissected blood-meals from fed, resting mosquitos were mixed with saline and examined under a microscope. Examination of mosquitos resting in a small stone building harbouring twenty domestic fowl showed that it was a resting place largely for *C. annulioris* and occasionally *A. gambiae*. Of 21 *C.*

annulioris dissected, 16 contained blood-meals with nucleated red cells and two contained meals of mixed nucleated and non-nucleated corpuscles. All of seven *A. gambiae* had fed on a host with nucleated corpuscles. In separate collections made from the cattle section of a normal hut, 444 blood-fed *A. gambiae* included only one with nucleated corpuscles in its blood meal, and all of 22 *A. funestus* and 15 *C. annulioris* had non-nucleated red cells. These findings indicate that where there are many fowl together and man and cattle are absent, fowl may be important hosts to *A. gambiae* and *C. annulioris* but fowl are rarely a source of blood to *A. gambiae* frequenting normal domestic huts in which both man and cattle are present.

Host-preferences of Mosquitos resting outdoors.

(a) *From natural Resting Places.*

About a third of the island at the centre is a large area of grassland with boulder ridges and scattered boulders. Deep erosion gullies drain into rivers near their sources. Rats, lizards, frogs and birds are the common vertebrates in this terrain. Unfed and small numbers of fed *C. annulioris* and *C. univittatus* can be taken from the banks of erosion gullies, and unfed *A. gambiae*, *A. funestus*, *A. rhodesiensis* Theo., *C. annulioris* and *C. univittatus* from caves which are usually at the head of an eroded gully or the source of a stream. The caves are kept moist by water constantly seeping through the roof and sides.

Coastal areas are inhabited by a wide selection of hosts. Nearly all villages are situated near the coast and are concealed amongst trees such as mango, *Anthocleista* sp., *Cassia siamea* and *Bridelia micrantha*, and heavily-pruned *Tricalysia corbisieri*, *Markhamia* sp., *Canthium vulgare* and *Rauwolfia caffra*. Boulders and rocks, rising to a height of 30 ft. and with caves, usually occur amongst trees near villages. The rocks are sometimes covered with *Alchornia cordifolia* which sprawls over them like a vine. Patches of grass with *Coleus* sp., *Oldenlandia herbacea*, *Leonotis nepetaefolia* and ferns, *Asplenium* sp., occur amongst the rocks. Trees in villages are often inhabited by three species of bat, the epauletted fruit-bat (*Epomorphorus wahlbergi*) which is the most common species, the yellow-winged bat (*Lavia frons*), a common species, and the less common tomb bat (*Taphozous mauritianus*). The small-eared hollow-faced bat (*Nycteris hispida*) is occasionally seen on *Alchornia* but more often in caves whose surfaces are dry and devoid of higher plant life. These caves are also inhabited by rock-rabbits (*Heterohyrax syriacus diesneri*), which are very common, agama lizards (*Agama atricollis*), monitor lizards (*Varanus niloticus*) and Grant's skink (*Mabuia striata*). Hedgehogs (*Atelerix pruneri*) are sometimes seen on grassy patches among the rocks

TABLE III.

Numbers of mosquitos found resting in a cave on the north coast near Bubanja village.

Species	Males	Females	Unfed	Fed	Half-gravid	Gravid
A. rhodesiensis Theo.	7	91	8	21	36	26
A. gambiae Giles	5	12	5	0	2	5
A. funestus Giles	0	2	1	0	0	1
C. univittatus Theo.	11	36	14	4	7	11
C. annulioris Theo.	1	2	2	0	0	0
C. poicilipes (Theo.)	0	1	1	0	0	0
C. tigripes Grp.	0	1	1	0	0	0
T. africanus (Theo.)	3	9	9	0	0	0
Aë. apicoargenteus (Theo.)	0	1	0	1	0	0
Aë. africanus (Theo.)	0	1	1	0	0	0

at dusk. Other possible hosts are birds, chiefly weaver-birds and bulbuls which nest in *Alchornia* lying over rocks and in *Cassia* and mango trees.

Mosquitos resting in a cave were collected by two Africans for six hours each day for ten days. For the same time four Africans collected mosquitos resting in grass, *Coleus* and *Asplenium* sp. at the base of rocks. Mosquitos in caves were collected in test-tubes with the aid of torches. Collections were made off grass and small plants by boys working in pairs. Each pair had a sheet of mosquito netting 6 ft. long by 3 ft. wide. This was spread over the ground and the vegetation gently beaten through the netting. The sides of the net were drawn together to envelop any mosquitos disturbed from the vegetation. The writer identified the mosquitos. The collections were made at Bubanja village on the north coast in June. The results are tabulated in Tables III and IV.

TABLE IV.

Numbers of mosquitos found resting on vegetation at the base of rocks on the north coast near Bubanja village.

Species	Males	Females	Unfed	Fed	Half-gravid	Gravid
A. rhodesiensis Theo.	1	10	5	0	2	3
A. gambiae Giles	1	0	0	0	0	0
A. coustani Lav.	1	2	0	0	0	0
C. univittatus Theo.	983	1029	742	37	132	118
C. annulioris Theo.	27	27	16	1	5	5
C. poicilipes (Theo.)	21	16	13	0	2	1
C. univittatus var. *neavei* Theo. ..	0	5	2	0	0	3
C. decens Theo.	1	8	6	0	1	1
C. antennatus (Beck.)	0	4	2	0	1	1
T. africanus (Theo.)	276	98	68	4	20	6
T. uniformis (Theo.)	22	16	11	0	3	2
Aë. africanus (Theo.)	0	1	1	0	0	0
Aë. aegypti (L.)	0	1	0	1	0	0

A. rhodesiensis and *C. univittatus* were the commonest species in caves in June and *C. univittatus* occurred in enormous numbers on grass and vegetation near rocks particularly from May to August. *T. africanus* replaced *C. univittatus* in abundance in November and December. Thus in a series of collections from crevices in rocks and from plants at the base of rocks at Bubanja in December there were 36 female and 32 male *T. africanus*, nine female and five male *T. uniformis*, 13 female and four male *C. univittatus*, six female *C. antennatus*, one female *C. poicilipes* (Theo.), one female and one male *C. annulioris* and one male *A. coustani* Lav. The change in the composition of the mosquito fauna is accounted for by the shrinkage in the breeding grounds of *C. univittatus*, such as rice-fields, and the extension of *Pistia* beds, in which *T. africanus* breeds, that occurs in Bubanja bay towards the end of the year.

Precipitin tests.—*A. rhodesiensis* resting in the type of cave just described, inhabited by rock-rabbits, bats and monitor lizards, feeds almost entirely on rock-rabbits. Of 68 blood-meals tested, 66 were positive for hyrax (rock-rabbit): 55 of these were tested for man, ox, goat, bat, rat, fowl * and hyrax, all of which live near or in the cave, and all the blood-meals were positive only for hyrax.

---

* Positives are obtained with anti-fowl antiserum for which serum for domestic fowl is employed. Positives are not restricted to domestic fowl blood but are not produced against blood of all species of birds.

A single blood-fed *A. gambiae* collected amongst rocks with vegetation was positive for man. The following numbers of Culicines, collected from crevices in rocks and in vegetation in the vicinity, were tested:

T. africanus: Of 32 tested for man, ox, goat, dog, rat, hyrax, bat and fowl three were positive for man, four for ox, one for hyrax and two for fowl.

T. uniformis: Of 29 tested for man and ox, four had fed on man and eight on ox. Of 25 tested for man, ox, goat, dog, rat, hyrax, bat and fowl, one had fed on man, seven on ox, two on goat and one on dog.

C. univittatus: Of 123 tested for man and ox, three had fed on man and 11 on ox. Of 28 tested for man, ox, goat, dog, rat, hyrax, bat and fowl, two had fed on ox, one on dog, two on hyrax and two on fowl. Of 57 tested for man, ox and hyrax, two had fed on man, four on ox, nine on hyrax and one on both man and hyrax.

C. annulioris: Of four tested for man and ox, one had fed on man and three on ox.

C. antennatus: Of eight tested for man, ox, goat, dog, rat, hyrax, bat and fowl, one had fed on ox.

C. poicilipes: Of ten tested for man, ox, goat, dog, rat, hyrax, bat and fowl, one had fed on man and goat, two on goat and one on fowl.

The large number of negatives, recorded above, may be accounted for in part by some blood-meals being inadequate for testing but, as smears subjected to precipitin tests were mostly large, the bulk of the negatives indicate the existence of unsuspected hosts.

Collections from natural resting places outdoors indicate that blood-fed *A. gambiae* and *A. funestus* are rarely found outdoors: there is no indication of their outdoor hosts, if any. It would seem, though, that *C. univittatus*, *T. africanus* and *T. uniformis* feed outdoors largely on hosts other than man and ox.

(b) *From artificial resting places.*

By digging a hole 8 ft. deep, 18 ft. long and 14 ft. wide with " pigeon holes " around the wall, a foot from the bottom, artificial outdoor resting places were made for mosquitos. The hole was dug near huts at Nyamanga village and the following numbers of mosquitos collected in daily examinations for ten days in July:—

A. longipalpis 38, *A. gambiae* 13, *A. funestus* 14, *A. rhodesiensis* 2, *A. rufipes* (Gough) 17, *A. maculipalpis* Giles 3, *A. coustani* 1, *C. annulioris* 4, *C. univittatus* 25. These findings are of interest because they indicate that *A. longipalpis* and *A. rufipes*, which are rarely found inside huts, rest chiefly outdoors although they were not found in collections amongst vegetation and at the base of rocks. Twenty-one of the 38 *A. longipalpis*, 9 of the 17 *A. rufipes*, 3 of the 13 *A. gambiae* and 2 of the 14 *A. funestus* were partly or completely blood-fed. The fact that we obtained blood-fed specimens from a hand-made pit, but rarely or not at all from natural resting places, suggests that blood-fed individuals of these four species may rest in narrow fissures in rock or holes in the ground, near villages, made by deep-burrowing animals such as termites or rodents.

Precipitin tests.—The following findings are from precipitin tests made on blood-fed mosquitos collected from the pit at Nyamanga and a similar pit at Bubanja. The specimens were tested against antisera of man and ox. Of 17 *A. gambiae*, 14 were positive for man and two for ox. Of three *A. longipalpis*, two were positive for man. All of four *A. rufipes* were positive for ox. One *A. funestus* tested was positive for man and one *T. africanus* for ox. Of 12 *C. univittatus*, two were positive for ox.

Dissections for nucleated and non-nucleated corpuscles in blood-meals of mosquitos taken in natural and artificial resting places outdoors.

Mosquitos from outdoor resting places were examined by the same method as described earlier in the paper. Ten blood-fed *A. gambiae* from hand-made pits near villages and seven *A. rhodesiensis* from a dark dry cave had non-nucleated corpuscles. Four *C. annulioris* from vegetation and four from hand-made pits had non-nucleated corpuscles. Of 14 *C. univittatus* from hand-made pits, 11 had non-nucleated corpuscles and three nucleated ones, and of 25 collected from vegetation outdoors, 20 had non-nucleated red cells and five nucleated ones.

The Feeding Reactions of Mosquitos to Small Animals in Cages.

In view of the possible existence of unsuspected hosts, and the occurrence of nucleated corpuscles in several species of mosquito, the studies were extended by the experiments described below. These were designed to test the response of various species of mosquito to a variety of common wild animals not covered by precipitin tests.

A. gambiae collected from the walls of huts, *Taeniorhynchus* species off human bait and *C. univittatus* off vegetation, were kept in cages surrounded with damp cotton-wool. While collecting these species, small numbers of other mosquitos were taken and were used in the experiments. Small lizards and bats were collected with the aid of a catapult and rock-rabbits and monitor lizards by a dog.

Except where otherwise stated, the technique is to starve the mosquitos for 24 hours in a cage surrounded with damp cotton-wool and a black cloth. The experimental host is put into the cage at night and removed the following morning. The mosquitos are then withdrawn and the numbers of unfed and gorged specimens of each species counted. When employing a rock-rabbit or a rat, the experimental animals are confined in stout wire cages which are inserted into the mosquito cages. Using this method it was found that, in the laboratory, *A. gambiae* feeds on rock-rabbit (*Heterohyrax syriacus diesneri*), multimammate rat (*Rattus coucha*), yellow-winged bat (*Lavia frons*), epauletted fruit-bat (*Epomorphorus wahlbergi*), African hedgehog (*Atelerix pruneri*), domestic chicken and African bullfrog (*Rana occipitalis*) but not on reptiles such as the agama lizard (*Agama atricollis*), Grant's skink (*Mabuia striata*), gecko (*Hemidactylus brookii*), or monitor lizard (*Varanus niloticus*). Two modifications of the usual technique were made, in the case of the epauletted fruit-bat and the frog, respectively. A six-inch wire mesh cage containing an adult and young *Epomorphorus* was put on a table in a mud hut. The cage was kept uncovered and the bats exposed to the mosquitos from 10 a.m. to 7 p.m. Out of 59 recovered, seven *A. gambiae* had fed, thus showing that *Epomorphorus* could act as a source of blood when confined with *A. gambiae* under conditions of subdued light during daytime.

In the first test with a frog it was noticed that many *A. gambiae* descended on the frog's skin, probed, and inserted the proboscis at the moment when the black cloth surrounding the cage was removed in the morning to examine the mosquitos. In a second exposure the cloth was removed at 8.30 a.m. and mosquitos examined through the wire mesh. None appeared to have fed. As in the first exposure, as many *gambiae* as 10 at a time alighted, made seeking movements and began to probe vigorously. At 10.30 a.m., 12 out of 93 had taken meals; of these, six were distended with a colourless liquid, five with straw-coloured fluid and one with what appeared to be undiluted blood. Most of the gorged mosquitos were observed during feeding which took place rapidly once the proboscis was inserted. Colourless fluid was taken from the eyes and straw-coloured liquid from the legs and back. A few mosquitos were macerated and their abdominal viscera smeared on microscope slides. Preparations were dried and stained with Giemsa. Those from *A. gambiae* with colourless meals showed many mononuclear lymphocytes and those with straw-coloured meals lymphocytes and some nucleated red cells. On a third occasion, of 108 examined, six *A. gambiae* had taken lymph meals and four of them meals containing lymph with some blood.

Only small numbers of *A. funestus* were collected from huts, but laboratory tests show that it will feed on the yellow-winged bat (*Lavia frons*) and on the multimammate rat (*Rattus coucha*). *Taeniorhynchus africanus* feeds avidly on

TABLE V.

The feeding reactions of mosquitos to small animals in cages.

Experimental host	No. of repetitions of expt.	Mosquito	No. recovered alive	No. fed
Rock-rabbit (*Heterohyrax syriacus diesneri*)	1	*A. gambiae*	224	42
		C. annulioris	2	0
		T. africanus	2	0
Multimammate rat (*Rattus coucha*)	1	*A. gambiae*	218	30
		A. funestus	7	1
Yellow-winged bat (*Lavia frons*)	3	*A. gambiae*	32	7
		A. funestus	4	2
		A. pharoensis	1	0
		T. africanus	12	12
		T. uniformis	12	11
		C. univittatus	12	7
		C. annulioris	2	2
		Aë. africanus	1	0
Epauletted fruit-bat (*Epomorphorus wahlbergi*)	1	*A. gambiae*	59	7
African hedgehog (*Atelerix pruneri*)	3	*A. gambiae*	45	1
Domestic chicken (4 and 6 weeks old)	2	*A. gambiae*	40	12
		A. funestus	2	0
		A. pharoensis	1	0
Agama lizard (*Agama atricollis*)	6	*A. gambiae*	161	0
		C. annulioris	3	0
		C. univittatus	14	4
Grant's skink (*Mabuia striata*)	1	*A. gambiae*	82	0
		A. funestus	2	0
Gecko (*Hemidactylus brookii*)	1	*A. gambiae*	3	0
		C. univittatus	2	1
Monitor lizard (*Varanus niloticus*)	2	*A. gambiae*	1	0
		A. pharoensis	1	0
		T. africanus	16	14
		C. poicilipes	1	1
		C. univittatus	8	3
		C. annulioris	3	2
African bullfrog (*Rana occipitalis*)	3	*A. gambiae*	207	22
		A. funestus	3	0
		C. univittatus	1	0
Green tree-snake (*Philothamnus semivariegatus*)	1	*C. univittatus*	6	1

the yellow-winged bat, which is also a laboratory host for *T. uniformis*, *C. annulioris* and *C. univittatus*. Lizards are fed on by *T. africanus*, *C. annulioris* and *C. univittatus*, the latter also feeding on the green tree-snake (*Philothamnus semivariegatus*). Details are shown in Table V.

In view of the fact that examples of *A. gambiae*, gorged with a colourless fluid, were occasionally taken in the field and that this species will take up lymph from frogs in the laboratory, this condition was investigated further. The river Nyamahesa (Smith, 1955*a*) swarms with frogs in April and May when *A. gambiae* is at its peak incidence. Small pits were dug at close intervals for about 50 yd. along the bank of the river in May and collections made from them in May and June. In 21 collections 87 female *A. gambiae* were found, of which 67 were unfed and 14 gravid. The remaining six contained colourless fluid in the abdomen. The collections also contained nine female *A. funestus*, 11 *A. rhodesiensis* and six *C. univittatus*. Single examples of *A. funestus* and *A. rhodesiensis* also had clear fluid in the abdomen. Smears of stomach contents of the mosquitos which had colourless fluid were stained with Giemsa. No mononuclear lymphocytes were present as in preparations from *A. gambiae* which had fed on frogs in the laboratory. It thus appears that the fluid in the abdomens of these species captured in the field is not derived from frogs but may be from some other source such as water, dew or nectar.

Summary.

Precipitin tests show that, on Ukara Island, Tanganyika, man and ox are the chief sources of blood to hut-resting mosquitos. *Anopheles gambiae* Giles and *A. funestus* Giles feed almost entirely on man. *A. pharoensis* Theo. feeds more on man than on ox. Culicines feed more on ox than on man.

Hand-catches off man, cow and goat in a hut confirm the results of precipitin tests on hut-resting mosquitos.

An account is given of the mosquito fauna of natural and artificial outdoor resting places and of the results obtained in precipitin tests on blood-fed mosquitos from outdoor resting places.

Blood-fed mosquitos resting indoors and outdoors were examined for nucleated red corpuscles in blood-meals. *A. gambiae* and *Culex annulioris* Theo. feed on domestic fowl.

Experiments in the laboratory, to find the facility with which different species of mosquito will feed on small wild animals of the island, show that *A. gambiae* and certain Culicines feed on a wide variety of hosts.

A. gambiae and *A. funestus* are incriminated as almost entirely responsible for the transmission of bancroftial filariasis on Ukara Island. A little transmission may take place by *A. pharoensis*.

Conclusions on the Transmission of Bancroftial Filariasis on Ukara Island, Tanganyika.

Vectors.

As a result of the observations in this and the previous papers of this series (Smith, 1955*a*, 1955*b*, 1955*c*) it is concluded that *Anopheles gambiae* Giles and *A. funestus* Giles are almost entirely responsible for the transmission of bancroftial filariasis of man on Ukara Island. The incriminating evidence is:—

1. *A. gambiae* and *A. funestus* comprise over 90 per cent. of the hut-resting mosquitos. There is a general coincidence in high densities of *A. gambiae* and *A. funestus* resting in huts and high incidences of bancroftial microfilaraemia in villages. Conversely, villages with low incidences of bancroftial microfilaraemia have low densities of hut-resting *A. gambiae* and *A. funestus*.

2. Nearly all villages with high incidences of bancroftial microfilaraemia are situated near rice-fields which are breeding grounds for these species. Villages with low incidences of bancroftial microfilaraemia are mostly situated away from rice-fields. There are a few exceptions but these can be explained when local conditions are taken into account.
3. *A. gambiae* and *A. funestus*, in contrast to other common mosquitos, bite indoors at night-time. This period coincides with the maximum microfilarial densities in man.

   Taeniorhynchus africanus (Theo.) and *T. uniformis* (Theo.) bite human "bait" freely outdoors. *Aëdes africanus* (Theo.) and *Aë. apicoargenteus* (Theo.) do not enter huts and they come into contact with people only for short periods during daytime, nor are they common during most months: their peak is between April and June.
4. Over 7,000 man-biting mosquitos have been examined for filarial infections. Proboscis infections have been found only in *A. gambiae* and *A. funestus*, although immature worms occur in *T. africanus*, *T. uniformis*, *Culex antennatus* (Beck.) and *A. pharoensis* Theo. The average infection rate, with infective forms, among 3,287 *A. gambiae* was 0·6 per cent. and among 1,228 *A. funestus* 1·0 per cent. Although the infection rates are low the inhabitants must be infected frequently because of sheer weight of numbers of adults of *A. gambiae* and *A. funestus*.
5. Precipitin tests on the blood-meals of hut-resting mosquitos show that, whereas *A. gambiae* and *A. funestus* feed almost entirely on man, other hut-haunting mosquitos such as *Culex annulioris* Theo. feed largely on cattle, which also form a large part of the diet of hut-resting *Taeniorhynchus* species. Precipitin tests on Culicines collected from their natural resting places outdoors show that outdoor hosts are an important source of blood. Not much is known about outdoor hosts of Culicines but we do know that rock-rabbits are a source of blood to *T. africanus* and *C. univittatus* Theo.
6. Findings on Ukara confirm those of West African workers that rural transmission of bancroftial filariasis is largely by *A. gambiae* and *A. funestus* (Gordon & others, 1932; Henrard, Peel & Wanson, 1947). Gordon & others incriminated *A. funestus* as at least as important a vector as *A. gambiae* because of the greater numbers of *A. funestus* in houses. *A. gambiae* would appear to be the principal vector on Ukara by virtue of its overwhelming numbers. Ninety-nine per cent. of hut-resting mosquitos in May and 75 per cent. in July are *A. gambiae*, whereas 0·6 per cent. of the May catch and 23·6 per cent. of the July catch are *A. funestus*. Also, an average of 200 *A. gambiae* can be taken off a man in a hut between 7 p.m. and 3 a.m. in May and 47 *A. funestus* between the same times in July (Smith, 1955*c*). Extensive rice cultivation between March and September, with widespread cultivation of an irrigated grass used as cattle fodder, gives rise to high seasonal incidences of the vectors.
7. *A. pharoensis*, which rests in huts and feeds more on man than on domestic animals, is heavily infected with immature filariae in the thorax. Owing to its short-lived peak in December and January it may be that most *A. pharoensis* do not survive long enough for the filariae to reach the infective stage.

Other filarial infections.

The present paper shows that *T. africanus* feeds on man, ox, rock-rabbit and fowl, *T. uniformis* on man, ox, goat and dog and *C. univittatus* on man, ox, dog, rock-rabbit and fowl. Precipitin tests also show that a small amount of mixed feeding occurs. There is a record of a specimen of *C. univittatus* positive for man and rock-rabbit and a single *A. longipalpis* (Theo.) for man and dog (Smith, 1955*a*). There is almost certainly no reservoir of *Wuchereria bancrofti* in domestic or wild animals but in view of filarial infections in dog and rock-rabbit as well as in man it is possible that infective filariae of non-human species of filarial worms are injected into man. The influence of such accidental transmission to man on his immunological reactions to infection with *W. bancrofti* is a matter for speculation.

A. rhodesiensis Theo., gorged with blood of rock-rabbits, occurs in caves. One would suspect this species as vector of the filarial infection which is found in 57 per cent. of *Heterohyrax syriacus diesneri* on Ukara (Smith, 1955*b*). The agama lizard (*Agama atricollis*) is abundant on Ukara and has a filarial infection (Smith, 1955*b*). It occurs in crevices in rocks in association with blood-fed *C. univittatus*. As some *C. univittatus* from rocks and vegetation nearby are found with nucleated corpuscles in their blood-meals, and as they feed on lizards in the laboratory, this species may be the vector of this filarial infection.

Acknowledgements.

I am grateful to Dr. Bagster Wilson, Director, East African Malaria Unit, for advice early in this work, to Col. W. Laurie, Director, Filariasis Research Unit, for fine equipment, to Mr. B. Weitz of the Lister Institute of Preventive Medicine who has carried out all precipitin tests gven in this paper, involving almost 2,000 mosquitos, and to Dr. D. S. Bertram, at the London School of Hygiene and Tropical Medicine, who kindly read and criticised the manuscripts of this series of papers.

References.

Gordon, R. M., Hicks, E. P., Davey, T. H. & Watson, M. (1932). A study of the house-haunting Culicidae occurring in Freetown, Sierra Leone. . .—Ann. trop. Med. Parasit., **26**, pp. 273–345.

Henrard, C., Peel, E. & Wanson, M. (1946). Quelques localisations de *Wuchereria bancrofti* Cobbold au Congo Belge. Cycle de développement chez *Culex fatigans* Wied., *Anopheles funestus* Giles, *Aedes aegypti* Linnaeus et *Anopheles gambiae* Giles.—Rec. Sci. méd. Congo Belge, no. 5, pp. 212–232.

Smith, A. (1955*a*). The transmission of bancroftial filariasis on Ukara Island, Tanganyika. I. A geographical and ecological description of the island with an annotated list of mosquitos and other arthropods of medical importance.—Bull. ent. Res., **46**, pp. 419–436.

Smith, A. (1955*b*). The transmission of bancroftial filariasis on Ukara Island, Tanganyika. II. The distribution of bancroftial microfilaraemia compared with the distribution of hut-haunting mosquitos and their breeding places.—Bull. ent. Res., **46**, pp. 437–444.

Smith, A. (1955*c*). The transmission of bancroftial filariasis on Ukara Island, Tanganyika. III. Biting-incidences on man and filarial infections in wild-caught mosquitos.—Bull. ent. Res., **46**, pp. 495–504.

THE PATTERN OF *GLOSSINA MORSITANS* COMMUNITIES.

By C. H. N. Jackson *

East African Tsetse and Trypanosomiasis Research and Reclamation Organisation, Shinyanga, Tanganyika.

In 1949 Mr. John Ford of this Organisation suggested that it might be illuminating if, instead of dividing our fly-rounds into sectors according to obvious vegetation types as we had been accustomed to do, we adopted a randomised system of catching stations at regular intervals (perhaps 50 or 100 yards), referring the flies to the actual stations at which they were captured and adding the vegetational details afterwards. It seemed that this useful suggestion might be improved by arranging the stations along a close spiral fly-round so as to sample an area rather than a band of country, and patches of equal apparent density of flies could then be joined across the rings of the spiral. At Daga-Iloi in Tanganyika, the site of this investigation, the rings of the spiral (fig. 1) were about 250 yards apart, the 75 stations were at 100-yard intervals, and the "spiral" was "octagonal" with successive paths turning at angles of 45°; it was always traversed anti-clockwise, that is, inwards towards the centre.

Such a spiral operated frequently would cause serious losses of male flies at least, unless they could be marked and liberated, and if so, it would be very desirable to know on recapture the date, station and other particulars of the fly when last released. A simple method of assigning distinctive marks to 25,000 individual flies was therefore devised (Jackson, 1953); such a system does of course lead to individual errors, so that there may be uncertainty about the history of any particular fly, but this applies to almost any system of marking, and when no more than a statistical result is aimed at the individual errors are not very important. Mistakes by African markers were satisfactorily few; they could most easily be observed where (Jackson, 1953) two species of tsetse were living together in sub-equal numbers, when any mistakes would be liable to cause a fly recorded as of the one species to appear as the alternate species (or sex) upon recapture. In practice, I found that suitable Africans made fewer mistakes than I did, and that most anomalies were due not to errors in marking, but to inattention in reading the marks on the recaptures.

The Country.

Daga-Iloi (pronounced by the local people more nearly as Daghwailui) lies at 4°11′S. latitude, 35°42′E. longitude, on a mass of gneissic hills plugging the Rift Valley between Ufiome Mountain (8,000 ft.) and the Rift Wall. The altitude in the working area varied from 3,900 to 4,800 ft., but the regular observations were within a smaller range (see fig. 1, where the contours were found from an aneroid barometer calibrated on various known heights and corrected for time of day). The climate is generally similar to that of Kikore (Nash, 1933), only some 20 miles away. The mornings at Daga-Iloi were, however, often quite cold, especially in wet weather during the rains and on the generally very cloudy mornings that persisted during the next three or four months, and it was the practice not to start the fly-round until the temperature rose to 21°C. (70°F.) or until 2 p.m., whichever was the earlier. On warm mornings the fly-round started at 9 a.m.; it was usually finished by 1 p.m.

---

* It is with great regret that readers will have learnt of the death of Dr. Jackson on 27th July 1955. Ed.

The vegetation of Daga-Iloi is extremely simple. The steeper hills and gentler slopes, all with numerous rock outcrops, are mostly wooded with well-grown *Brachystegia tamarindoides* (*B. microphylla* of Nash's paper). Under the spreading canopies of these fine trees grows a lower storey of much smaller ones, including *Combretum binderanum*, *Lannea schimperi*, *Commiphora fischeri*, *Hymenodictyon floribundum*, *Steganotaenia araliacea*, *Markhamia acuminata*, *Ormocarpum kirkii*, *Dalbergia stuhlmannii*, *Combretum gueinzii* subsp. *splendens*, *C. zeyheri*, *Commiphora pilosa*, *Lonchocarpus eriocalyx*, *Heeria reticulata*, *Terminalia hildebrandtii*, *Canthium burttii*, *Pavetta schumanniana*, *Acacia* cf. *holstii*, *Dichrostachys nyassana*, *Randia taylorii* and *Albizzia versicolor*. Visibility is usually upwards of 100 yards, as there is very little thicket. The grasses include *Digitaria marginata* (dominant), *Panicum maximum*, *Heteropogon contortus*, *Loudetia superba*, *Themeda triandra*, *Aristida* sp., *Chloris* sp., *Rhynchelytrum repens*, *Andropogon* sp., *Hyparrhenia* sp. and *Microchloa indica*.

On deeper soils with fewer rock outcrops are stretches of more open grassland with small trees, of which *Combretum zeyheri* and *Acacia* cf. *holstii* are the commonest. At higher elevations the grass is principally *Themeda triandra*, with the trees *Protea* sp., *Dombeya* sp., *Faurea saligna*, *Lannea schimperi*, *Acacia* cf. *holstii*, *Gymnosporia senegalensis*, *Piliostigma thonningii* (formerly *Bauhinia thonningii*), *Combretum gueinzii* subsp. *splendens* and *Securidaca longipedunculata*.

The deep ravines in the young topography of Daga-Iloi may be open with long grass, rocky with *Brachystegia tamarindoides*, or choked with dense and thorny, semi-evergreen thicket, flanked by *Acacia campylacantha* and topped by tall evergreen trees. The Daga-Iloi river itself has permanent springs and large trees of *Ficus* occur occasionally.

The Game Animals.

Like the vegetation, the big-game fauna of Daga-Iloi is a simple one. Roan antelope (*Hippotragus equinus*) and Coke's hartebeest (*Alcelaphus buselaphus cokii*) are the commonest large animals, but zebra (*Equus burchelli*) and buffalo (*Syncerus caffer*) appeared from time to time on the spiral. Waterbuck (*Cobus* sp.) were seen only on one occasion on the spiral. Bushbuck (*Tragelaphus scriptus*) were very common in all the ravines and their spoor on the paths of the spiral was more abundant than that of any other species; Bohor reedbuck (*Redunca redunca*) occurred in the long-grassed *Combretum* country, but common duiker (*Sylvicapra grimmia*) were the animals most frequently seen. Klipspringer (*Oreotragus oreotragus*) occurred on rocky hills, especially to the north, but were never noted on the spiral itself. Wart-hog (*Phacochoerus aethiopicus*) were fairly common, but bushpig (*Potamochoerus porcus*) were less frequent, passing through mainly in wet weather, and probably at night. Elephant (*Loxodonta africana*) and rhinoceros (*Diceros bicornis*) appeared occasionally.

A few miles away, about the village of Babati on the Great North Road, impala (*Aepyceros melampus*) and dikdik (*Rhynchotragus kirkii*) occurred in xerophytic thornbush in the rain-shadow of Ufiome mountain, but were never seen on the left bank of the Daga-Iloi river in this region. In the same way, the monkeys of Babati were all the little grey vervet, *Cercopithecus aethiops*, but at Daga-Iloi this species was never seen, and the only monkey was *C. mitis*, which was confined to the river. On the other hand, baboons (*Papio anubis*) occurred indiscriminately.

The area being closed because of sleeping sickness, man was very rare. Personally I only once saw people not directly connected with the work, except a party of man-hunting Mangati (Barabaig) awaiting in ambush the passage of the milkman; and a lady visitor was treed by a rhinoceros pursued by two local spearmen. In spite of this lack of man as an infecting agent, *Trypanosoma rhodesiense* was found on 8th June 1950 in the blood of one of my staff, who could not have picked it up more than a mile or two from the house (fig. 1).

The detailed distribution of the game animals (fig. 2) was studied mainly from records of spoor; the paths of the daily fly-round were hoed, and, except

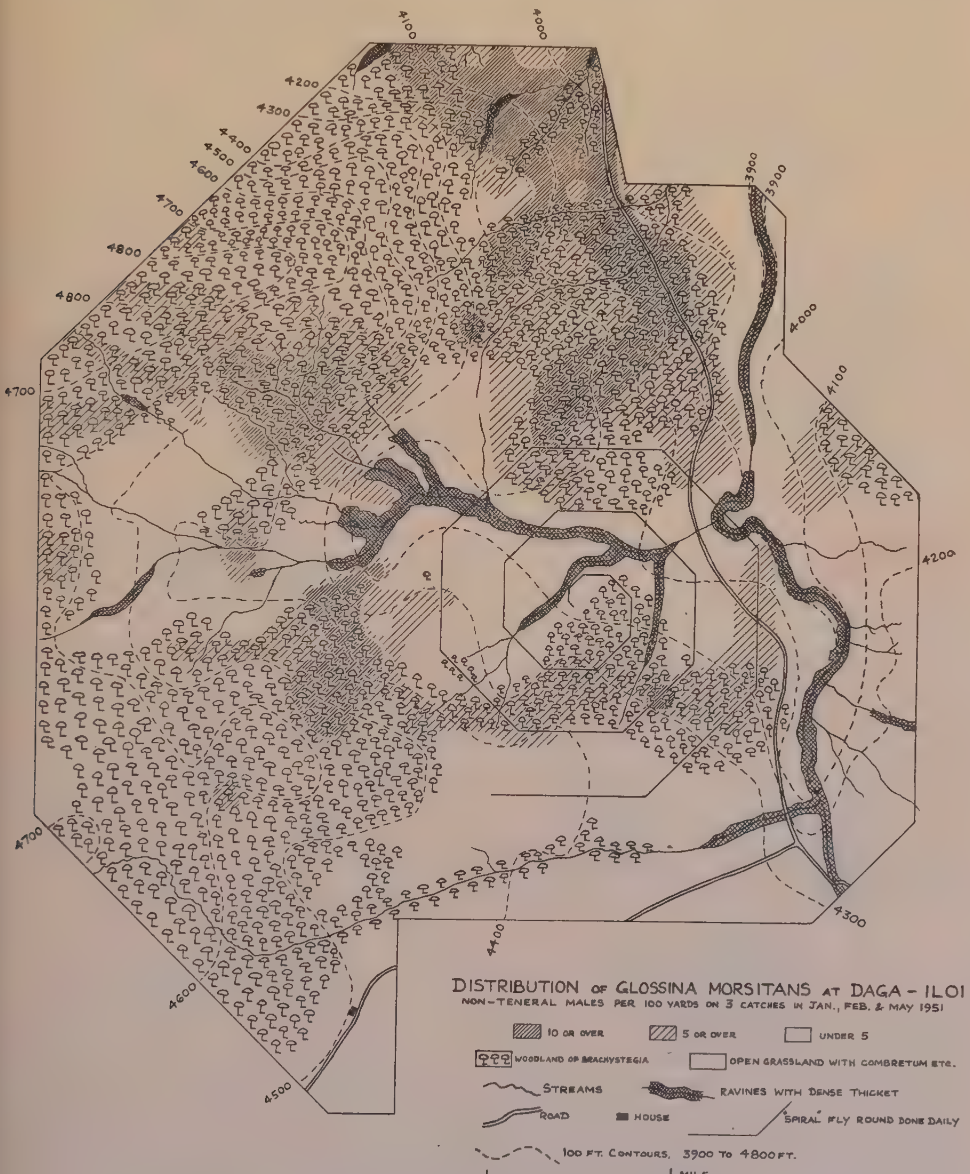

4100
4000
4200
4300
4400
4500
4600
4700
4800
4800
4700
3900
3900
4000
4100
4200
4300
4400
4700
4600
4500
DISTRIBUTION OF GLOSSINA MORSITANS AT DAGA - ILOI
NON-TENERAL MALES PER 100 YARDS ON 3 CATCHES IN JAN., FEB. & MAY 1951
10 OR OVER
5 OR OVER
UNDER 5
WOODLAND OF BRACHYSTEGIA
OPEN GRASSLAND WITH COMBRETUM ETC.
STREAMS
RAVINES WITH DENSE THICKET
ROAD
HOUSE
SPIRAL FLY ROUND DONE DAILY
100 FT. CONTOURS, 3900 TO 4800 FT.
1 MILE

Fig. 1.—Distribution of vegetation types and of *Glossina morsitans* at Daga-Iloi.

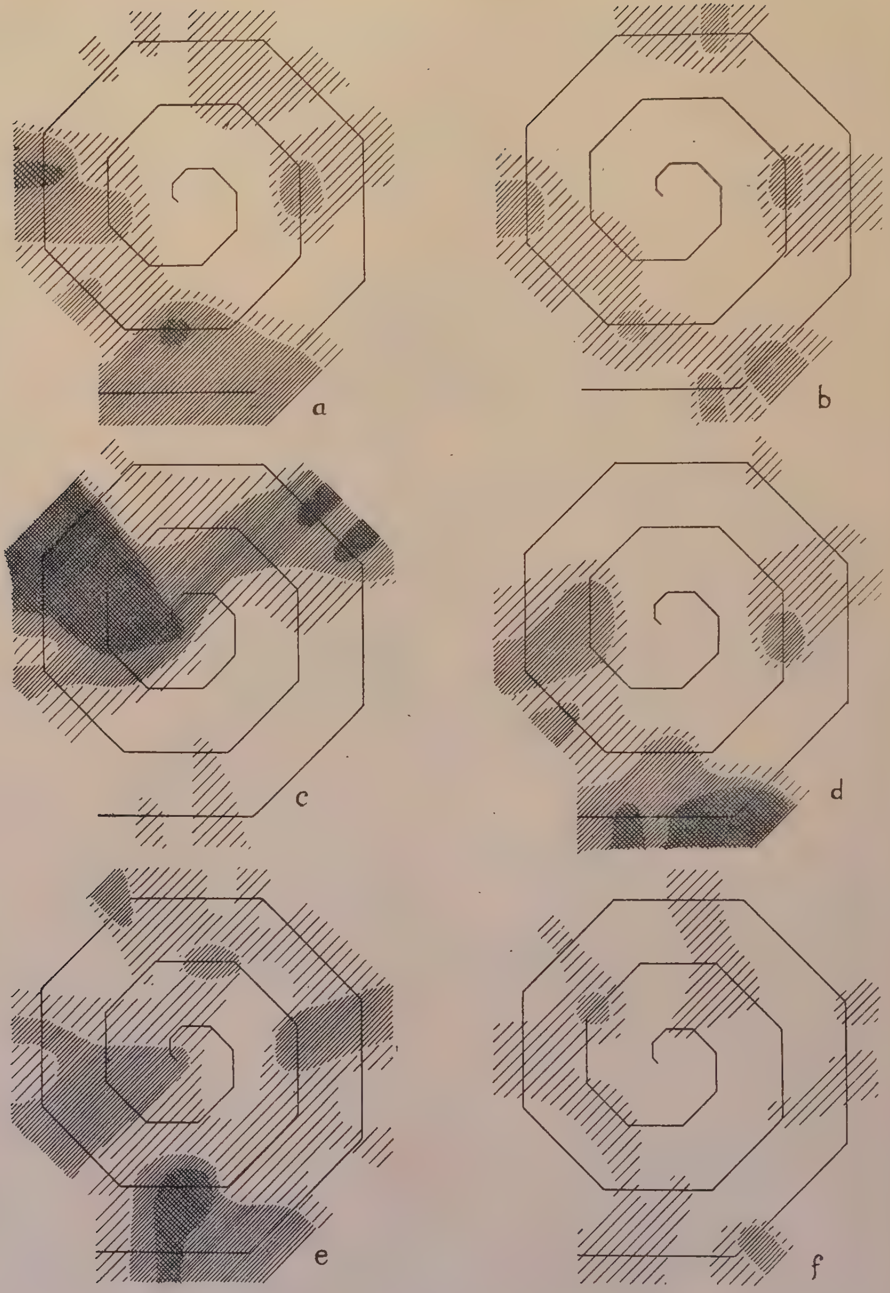


Fig. 2.—Occurrences of ungulate spoors at each station over a year, April 1950 to March 1951: cross hatch, 20 upwards; close hatch, 10 upwards; open hatch, 5 upwards; blank, below 5. (a) roan antelope; (b) hartebeest; (c) bushbuck; (d) reedbuck; (e) duiker; (f) wart-hog. Most of the animals are outside the *Brachystegia*, and the bushbuck are especially in the ravines.

for a month or so when the soil was hard after the rains before it broke up under the warm sunshine of the dry season, showed the hoof-prints of the animals fairly well. Spoors of Primates and Carnivora were not generally recorded; those of ungulates and elephants always were, but, as it was usually impossible to be sure how many animals made up a party, they were finally assessed only as occurrences, and not as individuals, along the 100-yard length of path leading up to each catching station.

The distribution on the spiral of the spoor records of the six commonest ungulates over a year (April 1950 to March 1951) is shown in fig. 2; fig. 5,c is the corresponding picture for all ungulates combined. Bushbuck (fig. 2,c) were commonest about the ravines, especially the one entering from the west side of the spiral, but in general all the species of ungulates were commonest outside the *Brachystegia* woodland, which has lower visibility and generally poorer grazing than the open *Combretum* on the east and west sides of the spiral and the *Protea-Faurea* grassland on its south limb.

The General Distribution of *Glossina morsitans*.

Glossina morsitans Westw. was apparently by far the commonest species of tsetse present and is the only one considered here. *G. pallidipes* Aust. was caught fairly frequently, mainly in drier weather and generally near the river or ravines. *G. swynnertoni* Aust. very rarely appeared on the spiral, ascending the valley from the Dudumera area several miles below.

The spiral proper (shown as a continuous line on fig. 1) was operated daily from late January 1950 to early May 1951, except on Sundays and except in March to early June 1950 when it was worked only on Monday, Tuesday, Thursday and Friday of each week. Towards the end of 1950, additional spirals, not shown in fig. 1, were added outside the original one, the last of them being completed in January 1951, after which each of the outer spirals was done at least three more times, namely mid-January, mid-February and early May. The general picture obtained from three traverses of the whole series of spirals is shown on fig. 1. It was not possible to do all of them on a single day, and the figures for the inner, daily spiral were chosen by taking the mean dates in January, in February and in May on which the outer rings were done. These outer rings were mostly incomplete on the east side, where the hills were steep and held few flies, and on the south side where the bush gave way to the derelict coffee plantation of Daga-Iloi.

Generally, it seems from fig. 1 that the flies (number of non-teneral males caught) tend to concentrate in *Brachystegia* woodland sloping not too steeply and not too far away from open grassland with small *Combretum* and *Acacia* trees. Thicketed ravines were avoided.

Fig. 1 also suggests that higher densities might have been observed on the inner spiral, done daily, had flies and game been as undisturbed as on the outer rings; the highest densities tended to occur outside the inner spiral, although some parts of this seemed perfectly suitable.

Seasonal Distribution of *G. morsitans*.

The seasonal distribution of *G. morsitans* could be studied only on a smaller scale (fig. 3, fig. 5,a). On the daily spiral there were two principal concentration areas, one in the *Brachystegia* woodland in the north-west and the other in the *Brachystegia* south-east of the centre. The first of these was the more persistent and formed (fig. 1) the fringe of a more extensive area of concentration. In neither of these two concentrations were the flies hungry; this can be seen from fig. 4 and fig. 5,b, which show the percentage of non-teneral males alighting head upwards on the catchers. most of which flies could be presumed to

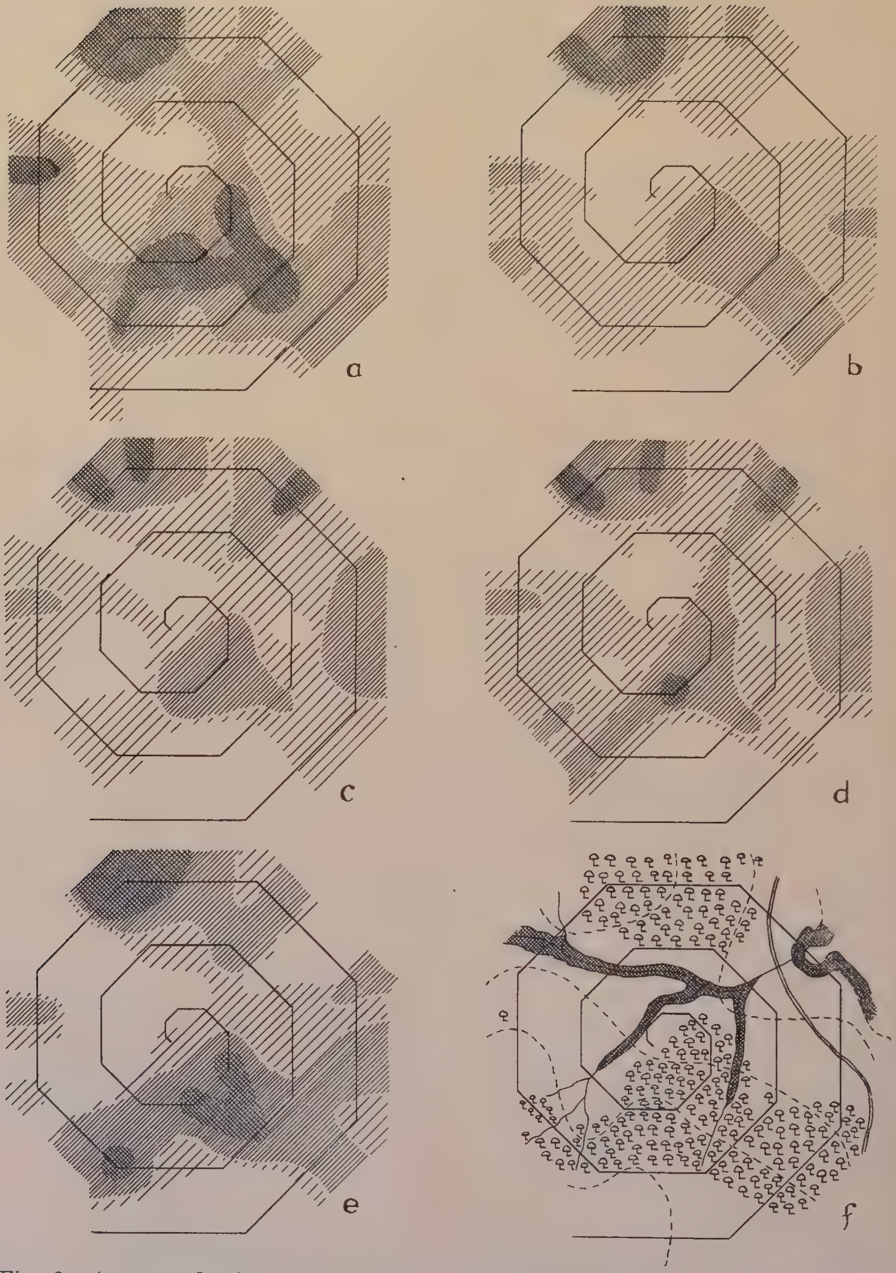


Fig. 3.—Apparent density (non-teneral males caught per 10,000 yards): cross hatch, 200 upwards; close hatch, 100 upwards; open hatch, 50 upwards; blank, below 50. (a) to (e) are for five consecutive three-month periods, starting with February–April 1950 and finishing with the same quarter of 1951; (f) repeats the vegetation from fig. 1. Note how concentrations of the first quarter tend to reappear in the fifth; also the persistent small concentration associated with a pair of large *Brachystegia* trees on the western boundary of the spiral.

be hungry. This percentage (Jackson, 1933) is not the best measure of hunger, but, as after the first three or four months only occasional rounds were conducted by me, it seemed best to rely upon a method that is at least objective, though hunger-staging was always done as well.

Grass fires burned most of the spiral in late September, and the two main concentrations dispersed; most flies were then taken at a station on the road (fig. 3,c) not far from the river, and rather more flies were then found in the neighbourhood of the river, though the gallery forest of the river and ravines continued to show much lower apparent densities than the *Brachystegia* woodlands. The two main concentrations found in the *Brachystegia* in the rainy season when the observations began both reappeared in the corresponding quarter of the following year (fig. 3, a & e).

At all times when well-marked concentrations existed in the *Brachystegia*, the most generally hungry flies were found, not only outside the concentrations themselves, but outside the *Brachystegia* woodland (fig. 4, fig. 5,b). Most of these hungry catches were made in the open grassland with small trees on the east and the west sides of the spiral; on the higher grassland with *Protea* and *Faurea* on the south side flies were also hungry, but, except quite close to the *Brachystegia* woodland, they were very few. Hunger, as usual, is evidently higher in the dry season. What is not so usual is that it was about as high in May to July (end of rains to start of dry season, fig. 4,b) as in the hotter part of the dry season from August to October (fig. 4,c) when the grass fires occurred. This observation is supported by direct estimation of hunger expressed in terms of the mean hunger stage (M.H.S.) (Jackson, 1933). In early 1951 (fig. 4,e) hunger was lower than a year before (fig. 4,a), perhaps because it was very much wetter. Particulars of the *G. morsitans* caught on the spiral are given in Table I.

TABLE I.

Catches of *G. morsitans* on the spiral, Daga-Iloi, Tanganyika.

	Apparent density	Percentage females amongst non-teneral flies	Percentage teneral males amongst total males	Percentage females amongst teneral flies	Percentage non-teneral males alighting head-up
1950					
February	137	8·3	8·1	50·3	33
March	119	4·1	3·1	50·0	18
April	101	4·2	4·2	48·1	24
May	105	8·4	11·2	47·5	28
June	83	14·0	16·2	46·2	35
July	81	13·3	14·7	49·0	41
August	83	12·1	13·5	41·5	37
September	66	22·4	26·8	42·6	38
October	85	23·7	13·8	48·5	36
November	64	12·9	8·3	56·0	23
December	68	11·9	10·4	50·0	21
1951					
January	111	11·0	8·2	55·6	18
February	91	7·7	9·8	45·9	18
March	91	7·8	9·6	49·2	20
April	108	6·6	3·9	50·0	20

Apparent Density (A.D.) = numbers of non-teneral males per 10,000 yards.

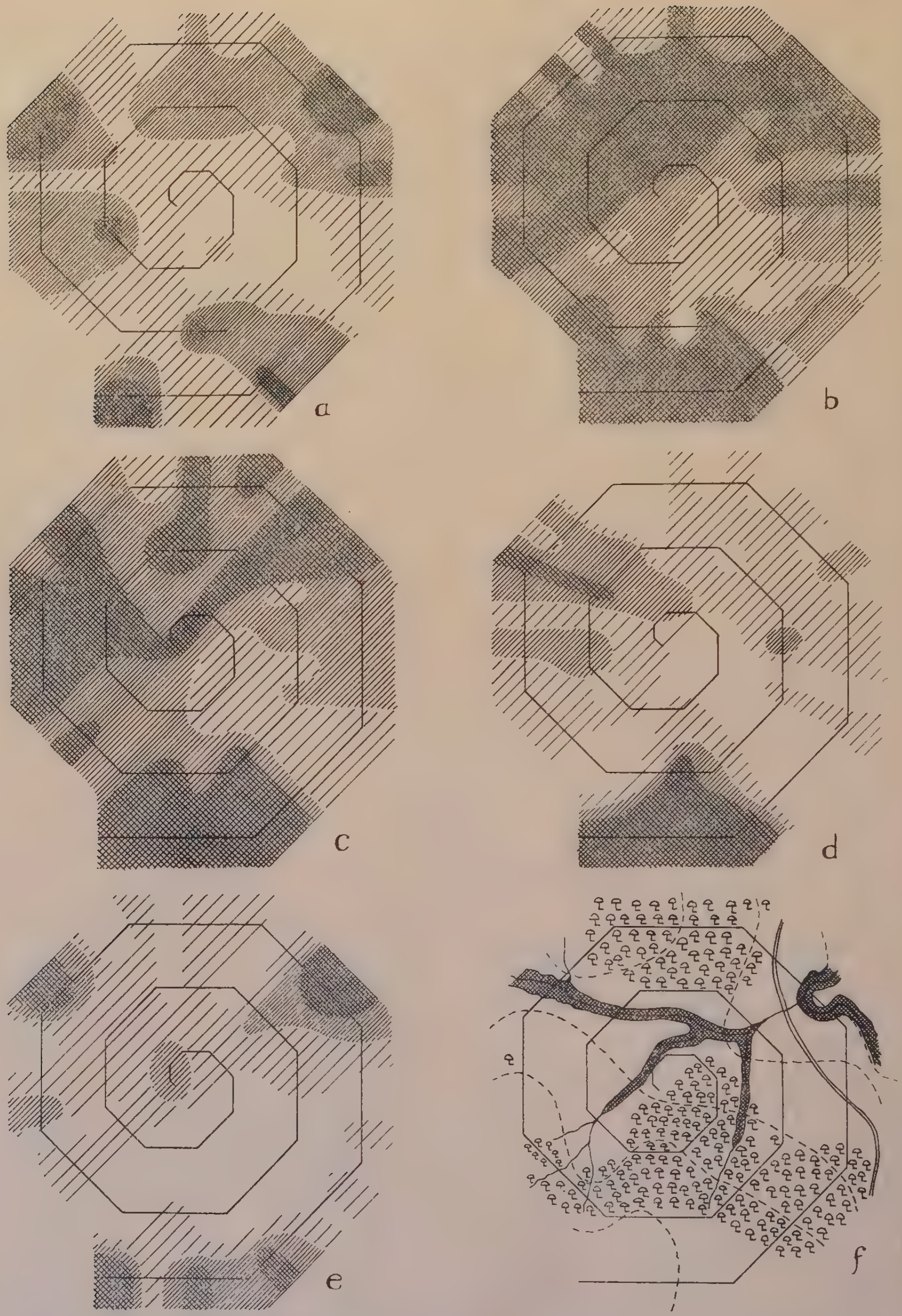


Fig. 4.—Hunger as judged by the percentage of non-teneral males alighting head-upwards on members of the catching party. (a) to (e) are for the same five consecutive quarters as in fig. 3 and (f) repeats the vegetation. Cross hatch, 40 upwards; close hatch, 30 upwards; open hatch, 20 upwards; blank, below 20. Note spread of hunger with arrival of dry season (b, c), its decline with the return of the rain (d) and the general resemblance of the fifth and the first quarters, except that hunger is generally lower in the fifth, which was very wet.

The Feeding-ground Theory.

A comparison of figs. 2 and 5,a with figs. 3 and 5,c shows that, species by species the game animals are most numerous where the flies (non-teneral males) are not. The coefficient of correlation of fly numbers with spoor numbers of each of the six commonest species of ungulates varies from about $-0\cdot2$ to $-0\cdot4$, and with all ungulates (and elephants) combined it is $-0\cdot47$ (fig. 5). In general the flies tend to be hungriest where the animals are most abundant (figs. 4 and 5,b): the coefficient of correlation between the percentage of non-teneral males alighting head up (fig. 5,b) and the total of ungulates and elephants (fig. 5,c) is $+0\cdot62$. Where animals are more numerous, therefore, flies caught are both scarcer and hungrier than elsewhere.

This paradox is in my experience very characteristic of *G. morsitans* distribution; the flies are commonest and best nourished in the homogeneous and

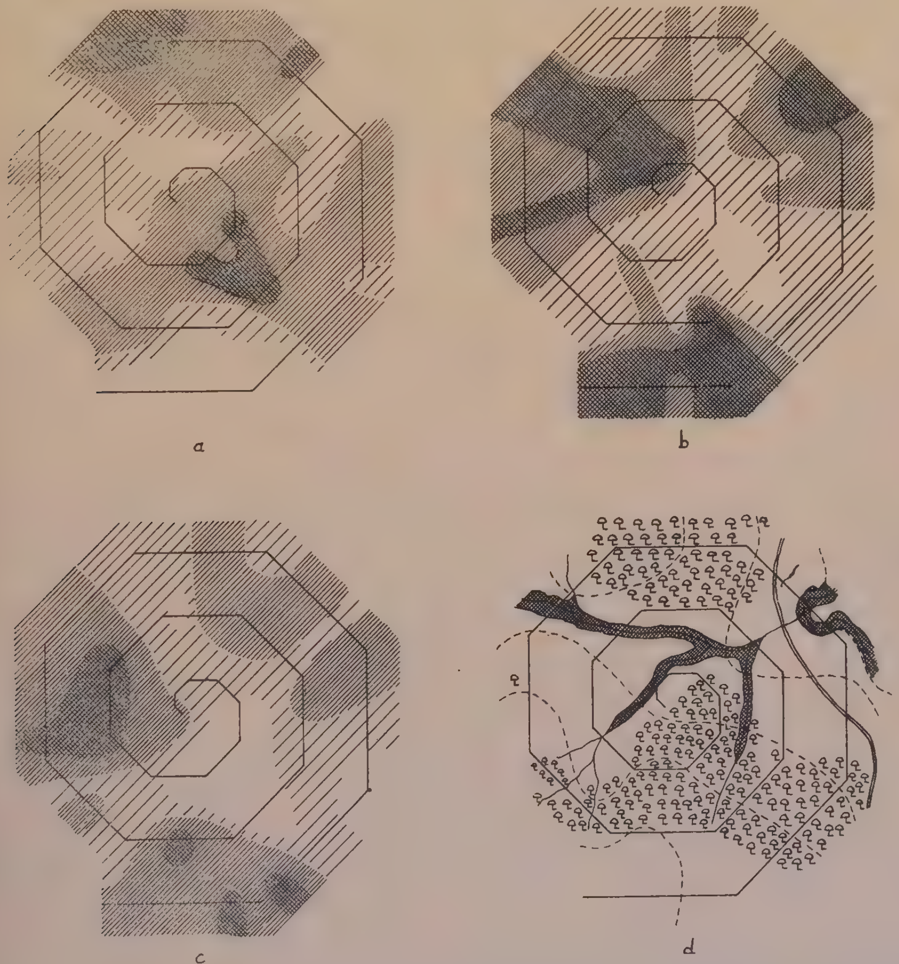


Fig. 5.—Apparent density of flies (a), hunger of flies (b) and occurrences of total ungulates (c) over the year, April 1950 to March 1951; (d) repeats the vegetation. Note negative correlation of apparent density of flies with game animals and positive correlation of game animals with fly hunger. The scale of hatching for (a) and (b) is the same, respectively, as for figs. 3 and 4. That for (c) is: cross hatch, 80 upwards; close hatch, 40 upwards; cpen hatch, 20 upwards; below 20, blank.

well-shaded *Brachystegia* woodland, with its generally poorer visibility and poorer grazing, while the animals are commonest in the open grassland, with better grazing and longer visibility, where flies tend to be scarcer, at least in the rains and hungrier than in the *Brachystegia* woodland. The present observations thus give factual backing to a general impression, which is also in harmony with the feeding-ground theory, according to which hungrier flies sally forth to find their food outside the shady *Brachystegia* that forms their proper home.

The movements of flies during February and March 1950, when I did virtually all the hunger-staging myself, are what one would expect on this theory. Bearing in mind Mr. Ford's recommendation to avoid subjective divisions into vegetation types, I divided all the stations on the spiral into those with M.H.S. under 3·0 (A), 3·2 or over (C) and intermediate (B), but excluding from the contributors to M.H.S. the recaptures about to be considered. Confining myself to recaptures which had changed their hunger stage within three days of release, I then tabulated, for February and for March separately, all those flies that had moved from type A to type C and *vice versa.* Flies that had gone from A to C tended to be recaptured in a higher stage of hunger (presumably losing weight) and those from C to A in a lower stage (presumably gaining):—

Change of station	Number of flies that:— Gained weight	Lost weight	Total
A to C	2	20	22
C to A	14	3	17
Total	16	23	39

Type A stations were all in the *Brachystegia* or on or very near its edge, and type C were in comparatively open country. Game spoors were most numerous in type C, intermediate in type B and scarcest in type A (approximately 0·3, 0·25 and 0·2 per station per day).

This result, though it does not prove the feeding-ground theory, is at least what would be demanded by it.

My colleague Dr. Einar Bursell has suggested that flies caught in " feeding grounds " may not really have been waiting there but have just flown out from the better shaded woodland or ecotone to attack the party as it comes into view. Nash (1933, p. 135) has also suggested that this is what happens, at any rate in hot weather. But, if so, one would perhaps always expect to find more flies in the ecotone than out in the relatively open grassland, whereas at seasons when flies are really hungry more are caught in the feeding ground than in the edge of the woodland (Jackson, 1934). Also, Lloyd (1935, Table XVI) did show that flies (*G. swynnertoni*) independently traversed a fenced and game-free clearing 800 yards wide, and that initially hungrier flies went across first. This seems to show that hungry flies do enter open country even when they cannot see any host-animals in it. Nash (1933) succeeded, though admittedly in the cool season, in inducing an artificial concentration of *G. morsitans* in open country, by making artificial paths which met at a waterhole not then being used by game. The whole question should, however, be carefully reconsidered, and if possible suitable experiments should be devised to show what really does happen.

Population and Dispersal of *G. morsitans.*

Population estimates were worked out for each month, using both the recapture and the re-recapture methods, but, except that the two methods agreed fairly well (*cf.* Jackson, 1953), the results are not of much interest. This is because, in unconfined places, such estimates refer to areas somewhat larger than those in which marking takes place, and where the marking area is small, as it was at Daga-Iloi, the unknown external portion which the population estimate includes is not only relatively large, but is also likely to vary greatly from season to season, depending on the ambits in which the loosely-distinct communities of flies are living.

One of the objects of laying out the spiral at Daga-Iloi was to watch for any mass movement of flies with herds of big game, especially buffalo. These lived mainly lower down the valley, and it was hoped that in ascending this they would sometimes pass right across the spiral (fig. 1), perhaps bringing flies with them or taking them away. Given a good population of marked flies on the spiral, either the addition of unmarked or the subtraction of marked individuals should then be easily detectable. The mathematical technique is to correct the recaptures both for numbers marked and for numbers caught on recapture days and to arrange them in a " Fisher lattice ", as explained in Glasgow (1953)—but by days instead of half-weeks. Lines are then drawn down at 45°, S.W. and S.E. from the date of passage of the animals; if the animals bring flies with them there will be an abrupt step-down in values of corrected recaptures when the former line is crossed from N.W. to S.E., and if they take flies away then there will be a similar step-down from N.E. to S.W. of the line running S.E. (see Tables II and III). On the seven occasions when herds of buffalo came, there was never any suggestion of many flies being brought in or taken away by

TABLE II.

Corrected recaptures of non-teneral male flies, Daga-Iloi, May 1950.
(Buffalo were present at 6 of the catching stations early on 15th May.)

MAY 1950

4		5		6		7		8		9		10		11		12		13		14		15		16		17		18		19		20		21		22		23
	30		.		.		.		7		.		.		12		.		.		.		5		.		.		8		.		.		.		23	
.		.		.		.		.		.		5		.		.		.		.		.		.		3		.		.		.		.		.		.
	.		.		8		.		.		8		3		.		.		2		.		.		4		1		.		.		4		.		.	
.		.		0		0		.		.		1		.		.		4		6		.		.		2		.		.		1		9		.		.
	.		.		0		.		.		.		.		.		.		2		.		.		.		.		.		.		5		.		.	
.		4		.		.		0		.		.		.		5		.		.		2		.		.		.		9		.		.		9		.
	2		0		.		0		3		.		.		7		5		.		5		4		.		.		2		2		.		2		2	
.		3		.		.		5		.		.		.		3		.		.		8		.		.		.		0		.		.		2		.
	.		.		0		.		.		.		.		.		.		6		.		.		.		.		.		.		0		.		.	
.		.		2		0		.		.		0		.		.		1		3		.		.		2		.		.		0		0		.		.
	.		.		1		.		.		0		3		.		.		3		.		.		2		2		.		.		0		.		.	
.		.		.		.		.		.		0		.		.		.		.		.		.		0		.		.		.		.		.		.
	5		.		.		.		0		.		.		3		.		.		.		3		.		.		0		.		.		.		3	
0		2		.		.		3		0		.		0		0		.		.		0		2		.		0		6		.		.		0		0
	6		.		.		.		0		.		.		4		.		.		.		0		.		.		0		.		.		.		0	
.		.		.		.		.		.		4		.		.		.		.		.		.		4		.		.		.		.		.		.
	.		.		0		.		.		1		0		.		.		0		.		.		1		0		.		.		0		.		.	
.		.		6		2		.		.		0		.		.		0		0		.		.		3		.		.		0		0		.		.
	.		.		3		.		.		.		.		.		.		0		.		.		.		.		.		.		0		.		.	

Obviously no effect

them, or, on the two occasions when they came, by elephants; but it may be that the animals came mostly at night.

On two occasions, however, large herds of buffalo visited the spiral by day, evidently early in the morning, and each time there was a marked rise of Stage I (gorged) and about a day later of Stage II (replete) flies in the neighbourhood of the stations through which the animals passed, indicating that many flies had fed on them.

Tables II and III are excerpts from the "Fisher lattice" of corrected recaptures round about these two dates. At the time of Table II, the fly-round was done on only four days a week, which accounts for the gappy appearance of this table; the fly-round from which Table III derives was done daily except on Sundays.

In Table II, the corrected recaptures of non-teneral males do not drop suddenly to the right of the left-hand line, nor suddenly to the left of the right-hand one; evidently therefore the buffalo neither brought in nor carried away many flies. In Table III, there is an indication of a discontinuity at the left-hand line, in that

TABLE III.

Corrected recaptures of non-teneral male flies, Daga-Iloi, April 1951.
(Buffalo were present at 15 of the catching stations early on 23rd April.)

APRIL 1951 MAY

12		13		14		15		16		17		18		19		20		21		22		23		24		25		26		27		28		29		30		1		2
	3		2		.		.		9		8		6		23		20		.		.		13		0		8		20		3		.		.		5		9	
4		1		.		13		.		5		0		3		3		.		9		.		23		14		7		2		.		6		.		5		5
	3		.		2		1		.		0		2		12		.		0		4		.		23		5		7		.		3		4		.		3	
2		.		4		2		4		.		3		0		.		7		0		0		.		5		4		.		3		2		3		.		7
	.		3		0		5		2		.		0		.		8		3		9		0		.		0		.		2		3		0		4		.	
.		3		0		2		0		4		.		.		0		0		12		0		1		.		.		4		2		5		0		4		
	2		4		3		3		0		2		.		22		0		3		4		0		1		.		5		5		2		6		3		8	
3		2		9		0		2		1		.		.		0		2		4		3		4		.		.		13		5		5		8		6		
	4		0		0		4		1		.		3		.		0		0		0		0		.		0		.		5		5		6		5		.	
16		3		3		4		2		.		0		4		.		4		3		5		.		4		2		.		13		8		3		.		3
	5		4		4		2		.		4		2		7		.		5		2		.		0		5		3		.		0		3		.		6	
7		6		0		0		.		0		2		2		4		.		8		.		3		7		5		2		.		0		.		0		4
	3		7		0		.		0		2		0		0		5		.		.		0		0		0		7		5		.		.		4		6	
7		2		6		.		0		0		0		2		1		1		.		0		0		5		0		6		3		.		10		6		8
	0		3		.		5		0		2		0		0		0		.		.		0		2		3		3		7		.		.		0		4	
0		0		.		0		2		2		0		2		2		.		0		.		2		2		6		0		.		0		.		23		
	0		.		0		0		2		2		2		0		.		0		0		.		0		2		10		.		4		0		.			
2		.		0		0		7		0		1		0		.		1		0		2		.		0		0		.		0		3		0				
	.		0		0		5		4		6		1		.		4		0		1		1		.		0		.		0		0		0					
		0		0		0		4		0		2		.		1		2		0		2		1		.		.		4		5		0						

Sums of values included in 6 × 6 lozenges: A (apex below 15th April), 93; B (below 22nd). 123; C (below 29th), 159; D (below 18/19th), 53; E (below 25/26th), 94.

A/D = 1·8 > B/E = 1·3, indicating a "possible" incursion of flies with buffalo.

On the other hand, C/E = 1·7 < B/D = 2·3, an "impossible" effect of about equal magnitude.

Note: The dotted line across the lower left-hand corner indicates the boundaries of two 6 × 6 lozenges, elsewhere shown as an empty "lane" which in this case was filled up because some marking had been done on a Sunday.

there is a sharper drop from lozenge A to D than there is from lozenge B to E. This might indicate that the buffalo brought flies with them on the morning of the 23rd; but the drop from lozenge C to E is actually less than the drop from lozenge B to D, indicating a "negative number" of flies removed when the buffalo left. The two effects, one "possible" and the other "impossible", are of about the same magnitude, and can thus indicate nothing more than errors of random sampling.

In these two examples there is, I consider, good evidence against the mass movement of fly communities with herds of buffalo. However, this story is so persistently urged, especially but by no means only in Uganda, that further observations are now being arranged there by my colleague Dr. J. P. Glasgow, both on these lines and on others.

Summary.

Tsetse flies (*Glossina morsitans* Westw.) were marked and released at Daga-Iloi, in Tanganyika on four or, usually, six days weekly for over 15 months, at 75 catching points situated 100 yards apart on an "octagonal spiral" whose successive rings were separated by 250 yards. Outer "spirals" were also traversed occasionally.

The country was hilly and dominated by woodland of *Brachystegia tamarindoides*, broken by more open grassland with *Combretum* on the one hand and by thicketed ravines on the other. The ungulate animals included zebra, buffalo, bushbuck, roan antelope, hartebeest, reedbuck, duiker, wart-hog and bushpig, with very occasional elephant, rhinoceros, waterbuck and klipspringer. Baboons and *Cercopithecus* monkeys were also present. Spoors of the ungulates were recorded on the daily rounds: bushbuck were most common about the ravines, but in general the ungulates tended to be most common in the open grassland with *Combretum*.

G. morsitans was most numerous in tall *Brachystegia* woodland where the slope was moderate, and where open grasslands were not too far away. Thicketed ravines were avoided. The highest apparent densities were observed on the outer "spirals", perhaps because of disturbance on the inner one traversed almost every day.

During the rains, well-marked concentrations of flies occurred in certain parts of the *Brachystegia* woodland, and these re-formed in the second year. The hungriest flies were always found outside the *Brachystegia*, and hunger was higher in the dry season. Hunger was measured objectively by the proportion of non-teneral males alighting head-upwards on members of the catching party, which hungry flies mostly do.

There was a negative correlation between numbers of flies and numbers of ungulates, and a positive correlation between the numbers of ungulates and hunger of the flies. This is in accordance with the feeding-ground theory, and is very generally observed with *G. morsitans* in East Africa. Certain movements of individual flies also accorded with the theory, against which, however, the suggestion has now been made that flies caught in the putative feeding grounds have not ventured out into them until attracted there by the sight of the catching party. This suggestion is to some extent countered by quotations from previous work, but it deserves further thought, and carefully planned experiments.

Passage of large herds of buffalo through portions of the "spiral" were not apparently accompanied by mass movements of flies, even when the animals passed by day and many flies fed on them.

Acknowledgements.

I am grateful to my colleague, Mr. J. M. B. Harley, for taking over the records from about February 1951, and for looking after all the work on my

Increased acceptances of non-teneral males indicates that

departure in March of that year; to Mr. K. S. Hocking, Officer-in-Charge of the Colonial Insecticides Research Unit of East Africa, for generously sending an aircraft to photograph the "spiral", and for presenting me with the double set of prints; to the District Commissioner of Mbulu, Mr. G. T. Bell, O.B.E., for placing at my disposal the house on the estate of Daga-Iloi; and to Mr. G. R. Jewell for drawing the maps for this paper.

References.

GLASGOW, J. P. (1953). The extermination of animal populations by artificial predation and the estimation of populations.—J. Anim. Ecol., **22**, pp. 32–46.

JACKSON, C. H. N. (1933). The causes and implications of hunger in tsetse-flies.—Bull. ent. Res., **24**, pp. 443–482.

JACKSON, C. H. N. (1934). A note on the concentrations of tsetse-flies.—Bull. ent. Res., **25**, pp. 457–458.

JACKSON, C. H. N. (1953). A mixed population of *Glossina morsitans* and *G. swynnertoni*.—J. Anim. Ecol., **22**, pp. 78–86.

LLOYD, H. M. (1935). Notes on the bionomics of *Glossina swynnertoni* Austen.—Bull. ent. Res., **26**, pp. 439–468.

NASH, T. A. M. (1933). The ecology of *Glossina morsitans* Westw., and two possible methods for its destruction.—Bull. ent. Res., **24**, pp. 107–157, 163–195.

THE HOST-ANIMALS OF *GLOSSINA MORSITANS* AT DAGA-ILOI.

By B. Weitz
Lister Institute of Preventive Medicine, Elstree, Herts.

and

C. H. N. Jackson *
East African Tsetse and Trypanosomiasis Research and Reclamation Organisation, Shinyanga, Tanganyika.

D O

During the year April 1950 to March 1951, 378 stomach smears of *Glossina morsitans* Westw. were collected on the spiral fly-round at Daga-Iloi, Tanganyika (Jackson, 1955). The flies were nearly all males and were in what is known as Stage 1 of hunger; that is to say, the blood was visible externally. The stomach contents were expressed on to filter papers and were examined upwards of a year later for the presence of blood from the various host-animals known to have been present, from spoor records or direct observation, on the fly-round.

Methods.

(a) *Extraction of smears.*

The feeds, which had been dried on the filter papers over calcium chloride, were each assigned a quality index number, 1 representing the quality of a feed an hour or two after ingestion, and 12 denoting an absence of visible blood (Table IV). They were then extracted by cutting out the blood smear from the filter paper and allowing the serum proteins to dissolve at 4°C. for about 12 hours in 1·0 ml. of 0·9 per cent. solution of sodium chloride. During the period of testing, which was about 18 days, the feeds were kept at 4°C. Where the quality of the feed permitted, only a portion of the smear was cut out for extraction, leaving sufficient dried material for subsequent testing should the first answer be inconclusive.

(b) *The precipitin test.*

This was carried out in narrow glass tubes of approximately 2 to 3 mm. internal diameter. About 0·05 ml. of the extract was first aspirated into the upper part of the tube and the antiserum was then drawn up below it in such a manner as to avoid mixing of the fluids and to obtain a neat interfacial juxtaposition of the extract and the antiserum. The fly extract was always tested with undiluted antiserum. The operation was done by means of a special apparatus to be described in a work under preparation (by B. W.). The tubes were allowed to stand at room temperature for 2 hours and examined against a dark background by transmitted light for the presence of a " ring " of precipitate at the junction of the two fluids.

(i) *Antisera prepared in rabbit.*—Rabbit *absorbed* antisera were prepared as described by Weitz (1952). The highest dilution of the homologous antigen which reacted positively with each antiserum is shown in Table I. Each antiserum had been absorbed so that cross reactions between the various groups of listed animals were absent, even with high concentration of serum (1 in 10) and after a period of incubation of two hours.

---

* It is with great regret that readers will have learnt of the death of Dr. Jackson on 27th July 1955. Ed.

(ii) *Antisera prepared in Bovids.*—A number of species of Bovids, including calves, sheep, goat and various antelopes, were inoculated with the serum of various related Bovids in an attempt to obtain monospecific antisera. Antisera prepared in this way, by " cross immunising " a species with the serum of a relative, have been shown to be specific, as, for example, when sheep proteins were inoculated into goats and produced monospecific anti-sheep serum; conversely, specific anti-goat serum was obtained from sheep inoculated with goat serum (Weitz, 1952).

TABLE I.

Sensitivity and specificity of absorbed rabbit antisera for the animals occurring at Daga-Iloi.

Antiserum	Serum	Reciprocal of titre of antigen
Anti-primate	Man	64,000
	Baboon	32,000
	Monkey	32,000
Anti-pig	Wart-hog	128,000
	Bushpig	?
Anti-horse	Zebra	32,000
Anti-rhinoceros	Rhinoceros	64,000
Anti-elephant	Elephant	32,000
Anti-hyrax	Hyrax	64,000
Anti-rat	Rat	64,000
	Swamp rat	64,000
	Mouse	8,000
Anti-porcupine	Porcupine	16,000
Anti-bovid	Buffalo	10,000
	Bushbuck	10,000
	Reedbuck	8,000
	Roan antelope	16,000
	Hartebeest	20,000
	Duiker	16,000
	Waterbuck	10,000
Anti-hartebeest	Hartebeest	16,000
Anti-mammal	Most mammals	16,000 to 128,000

Since the antigenic relations of the serum proteins of the various Bovids do not necessarily correspond with known zoological relationships, it was necessary to discover, by trial, suitable species of Bovids for inoculation with the serum of others. After many experiments four monospecific antisera were obtained: an anti-buffalo serum from sheep, reacting with the serum of buffalo alone at a dilution of 1/8,000; an anti-reedbuck serum prepared in a goat, reacting with reedbuck serum diluted 1/4,000; an anti-impala serum from sheep, reacting with impala serum at a dilution of 1/4,000; and an antiserum prepared in calves, reacting equally with the sera of kudu, eland and bushbuck at 1/5,000 dilution. These antisera, although usable at these titres, were difficult to preserve and their potency dropped considerably even when frozen at –15°C. Unlike antisera prepared in rabbits which were all dried successfully from the frozen state, the Bovid antisera lost precipitating potency on freeze-drying. By the time tests on fly meals were started the anti-impala serum was useless, reacting non-specifically with fly meals that did not contain impala blood.

(c) *The inhibition test*.—A new technique, to be described in a work under preparation (by B. W.), was used for monospecific tests, namely the inhibition of agglutination of tanned red blood cells. When normal rabbit red blood cells are treated with tannic acid and coated with the serum proteins of a given animal, they are agglutinable by an antiserum prepared against these proteins. The reaction, like the precipitin reaction, is not very specific, but its inhibition by a solution of one of the serum proteins under test is quite specific under certain conditions. Thus an unknown blood meal can be identified by adding a saline extract of the meal to a series of agglutinating antisera, A, B, C, D, which are then tested with a series of tanned red cell suspensions coated with the serum of the respective species A, B, C, D. The origin of the meal is identified from the particular system which the meal extract inhibits. This test was used for the identification of some of the blood meals of the flies from Daga-Iloi a year and a half after the completion of the precipitin tests. Unfortunately it was not possible to apply it to all of them because some of the dried smears had already been used completely.

(d) *Procedure*.—All blood meals were tested with anti-primate, anti-suid and anti-bovid rabbit antisera by the precipitin test. Those which reacted with the anti-primate serum and from which material was still obtainable were retested by the inhibition test to determine the individual species of origin, namely man, baboon, or monkey. Similarly feeds which reacted with anti-suid antiserum were tested for the presence of wart-hog and bushpig by the inhibition technique. The feeds reacting with anti-bovid serum were retested by the precipitin test with antisera prepared in Bovids for the presence of bushbuck, buffalo or reedbuck antigens. The presence of hartebeest antigen was similarly tested by the rabbit antiserum (Table I) which was the only monospecific rabbit antiserum used against Bovids. Later on a number of these feeds were retested by the inhibition test for the presence of buffalo, reedbuck, roan antelope, duiker and waterbuck blood, when the quality of available material permitted.

The feeds which failed to react with anti-primate, anti-suid or anti-bovid antiserum were then further tested by precipitin tests with rabbit antisera for the presence of the antigens of rat, porcupine, hyrax, elephant, jackal or hunting dog (*Lycaon*), hyaena, mongoose, cats (including lion and leopard), rhinoceros and zebra.

Some non-reacting feeds were tested with a rabbit antiserum that reacted with the sera of all mammals present in the area but not with any bird serum tested.

(e) *Validity of the tests*.—The precipitin test using antisera prepared in Bovids was used with the knowledge that, although its specificity might be complete, its relative insensitivity meant that a fair proportion of feeds would not be identified although they had in fact been derived from the species tested for, whereas positive results definitely indicate the presence of blood from the species concerned.

A preliminary trial on known feeds was made to estimate the reliability of the rabbit precipitating antisera and of the new inhibition test, when applied to field material. Wild flies (*G. swynnertoni* Aust.) were fed on bloods of man, ox, donkey, domestic pig and Thomson's gazelle; they were marked, released and recaptured after about a day at large. Smears were made from their stomach contents in the usual way and were examined by precipitin tests for the presence of Primates, Equidae, Suidae, antelopes and ox. The inhibition test was then applied to the appropriate group to test for man, baboon, monkey; horse, donkey, zebra; domestic pig, wart-hog, bushpig; Thomson's gazelle, duiker, impala or reedbuck. The source of the samples was unknown to the operator until after the completion of the tests.

TABLE II.

Identification by precipitin and inhibition tests of 28 known feeds of *Glossina swynnertoni*.

Number of feeds	Precipitin test	Inhibition test	Actual feed
6	Primates	5 man, 1 doubtful	Man
8	Equidae	8 donkey	Donkey
5	Suidae	4 domestic pig, 1 doubtful	Domestic pig
6	Antelopes	5 Thomson's gazelle 1 doubtful	Thomson's gazelle
3	Ox or relative	No tests	Ox

The results in Table II show quite clearly that the precipitin test with absorbed antisera made in rabbits was capable of distinguishing the main groups —Primates, Suidae, Equidae and Bovidae—and could distinguish the blood of ox from that of Thomson's gazelle; where, as in nearly all cases, the samples were adequate for testing by the inhibition of agglutination, this method correctly determined the individual species within the main groups. The results fully justified the use of the inhibition test for specific determination of the fly-meals at Daga-Iloi even after digestion had proceeded in the wild state up to about a day.

Results.

(*a*) *Identification by precipitin reaction.*

A few of the flies at Daga-Iloi had taken double feeds, so that a total of 378 flies gave a total of 383 meals.

Tests with appropriate sera indicated the absence of feeds on zebra, elephant, hyrax, hartebeest, bushbuck, rats, porcupine, mongoose and cat, including lion and leopard.

(b) *Identification by inhibition test.*

As already mentioned, inhibition tests were carried out only on a proportion of feeds, of which sufficient material was available. Of the Primates, 18 were identified as man, nine as baboon and none as monkey, and of 61 Suidae, 55 were determined as wart-hog and six as bushpig. The feeds from Bovidae are less straightforward, because the hartebeest and bushbuck, all of which had been negative by the precipitin test, were not subjected to the inhibition test; roan antelope, duiker and waterbuck were tested for by inhibition alone; only those reedbuck feeds found positive in the precipitin tests were retested by inhibition; buffalo feeds were discovered mainly by precipitin tests, but some were found by inhibition tests afterwards. It is sufficient to state that of 13 buffalo feeds found by precipitin tests, eight were confirmed by inhibition tests and a further eight were discovered; of five reedbuck feeds found by the precipitin reaction four reappeared in the inhibition test; and the inhibition test brought to light 17 feeds on roan antelope and one on duiker, but none on waterbuck.

From fly No. 158 onwards, samples of fresh blood were obtained by dabbing a glass slide on each filter paper smear; the slide smears were then fixed and stained with eosin in methyl alcohol and examined microscopically for red blood corpuscles. In 189 of the samples it was possible to identify the corpuscles as nucleated or not. Nucleated red cells were found in three of the slides, or 1·6 per cent. of the 189 recognisable smears. These three samples were among those found to be " unidentified " by the precipitin test.

TABLE III.

Results of precipitin tests on 378 *Glossina morsitans* from Daga-Iloi.

Group	Number
Primates	40
Suidae	172
Bovidae Buffalo	13
Reedbuck	5
Unidentified Bovids	95
Rhinoceros	3
Hyaena	2
Jackal	2
Unidentified	51
Total feeds ..	383

Discussion.

Since not all the fly-meals were tested by all the methods, it is necessary to adjust some of the above results in order to arrive at some idea of the proportions in which different host-animals were used for food. In particular, it is necessary to decide how many of the " unidentified " feeds in Table III were probably mammalian, how many non-mammalian and how many were probably unidentifiable through being of inferior quality. These " unidentified " feeds were generally of poorer quality than the remainder, as is shown by the quality indexes assigned to them (Table IV).

TABLE IV.

Quality indexes assigned to feeds, from 1 (best possible) to 12 (absence of visible meal).

Grade	1	2	3	4	5	6	7	8	9	10	11	12	Total
Identified ..	0	1	3	8	30	97	88	60	32	9	0	0	328
Unidentified ..	0	0	0	0	1	2	9	13	16	6	1	1	49*

* Only 49 of the 51 unidentified feeds appear in this Table because 6 feeds did not receive index numbers.

If we may take it that 1·6 per cent. of feeds are on nucleate blood, as is suggested by the 189 samples examined, then six of the 383 feeds are nucleates. Seventeen of the 51 unidentified feeds were tested by a general mammalian antiserum and five were positive. Had all 51 been tested, about 15 might have thus been expected to react with general mammalian antiserum, leaving 36 possibly avian or reptilian instead of only the six indicated by the microscopical examination. It appears, therefore, that perhaps 30 out of the 51 unidentified bloods were of too poor quality to react with anything, so that of the total of 383 feeds only 353 were in a state to allow their determination.

The 40 Primates may be apportioned to 27 feeds on man and 13 on baboon, and the 172 Suidae to 155 on wart-hog and 17 on bushpig, which are the values based on the successful inhibition tests applied to 27 Primates and 61 Suidae.

The total feeds may now be distributed as shown in Table V.

TABLE V.

The distribution of the origin of the fly-meals identifiable by precipitin or by inhibition tests.

Species	Total	Per cent.
Man	27	7·6
Baboon	13	3·7
Rhinoceros	3	·8
Wart-hog	155	44·0
Bushpig	17	4·8
Bovidae	113	32·0
Hyaena	2	·5
Jackal	2	·5
Other mammals ..	15	4·2
Birds or reptiles ..	6	1·7
	353	99·8
Unidentifiable	30	
	383	

The Bovidae include buffalo, roan antelope, reedbuck and duiker, but not apparently bushbuck, hartebeest or waterbuck. Apparently zebra are not fed upon. The "other mammals" may have been bats, insectivores or antbear, as these smears failed to react with the antisera of any of the other mammals present.

Elephant do not appear in Table V, but they passed through the area only once, apparently at night. Two of the three rhinoceros feeds came from a time when one of these animals had walked about a great deal on the spiral fly-round, and nearly all the 21 buffalo feeds discovered come from two occasions when large herds of buffalo had visited the spiral.

The most remarkable feature of Table V is the predominance of wart-hog and bushpig, and this is the more extraordinary when one considers the relative numbers of the Suidae of which, on spoor records, bushpig formed about a sixth.

The Equidae were zebra, and one recalls that Harrison (1940) always failed to see *G. swynnertoni* feeding on zebra at 50 yards, though plenty of flies were present, and he did on many occasions observe them on giraffe and wart-hog. Symes & McMahon (1937) examined 1,369 flies from Harrison's area by the precipitin test, and found none positive to zebra. On the other hand, one of us (C. H. N. J.) has caught both *G. morsitans* and *G. swynnertoni* on zebras that he has shot.

TABLE VI.

The incidence of families of ungulates in the area from spoor records compared with the incidence determined from fly-meals.

Family	Observed Spoors %	Identified blood meals %
Equidae	5	0
Rhinocerotidae ..	2	1
Suidae	10	60
Bovidae	84	39
	101	100

As to Suidae, it was noted (Jackson, 1940) that measuring blood cells from stomachs of *G. morsitans* indicated that 60 per cent. of all meals appeared to be derived from pigs, and it was suggested that so large a proportion might imply a physiological need for pig blood every second or third meal. The large proportion feeding on pigs is now confirmed, and Table VI suggests that pigs were about 13 times $\left(=\frac{60 \times 84}{10 \times 39}\right)$ more liked, or more available, than Bovidae.

The absence of bushbuck and hartebeest feeds is surprising, particularly as bushbuck was, on spoor records, the commonest ungulate on the spiral fly-round, and hartebeest was also very common.

The area was closed because of sleeping sickness and it is likely that nearly all the feeds on man were derived from African staff and labour employed on the work; it is thought to be improbable that *G. morsitans* there would ordinarily draw so much as 7 per cent. of its meals from man.

Summary.

Blood smears from 378 examples of *Glossina morsitans* Westw. from the Daga-Iloi fly-round were tested by serological methods, including a new test involving the inhibition of agglutination of tanned red blood cells.

About half the feeds were derived from wart-hog or bushpig, though these apparently formed only some ten per cent. of the ungulate mammals present.

References.

Harrison, H. (1940). The game experiment.—Tsetse Res. Rep., 1935–38, pp. 27–30. Dar-es-Salaam, Govt. Printer.

Jackson, C. H. N. (1940). An outline of experiments at Kakoma.—Tsetse Res. Rep., 1935–38, pp. 11–15. Dar-es-Salaam, Govt. Printer.

JACKSON, C. H. N. (1955). The pattern of *Glossina morsitans* communities.—Bull. ent. Res., **46,** pp. 517–530.

SYMES, C. B. & McMAHON, J. P. (1937). The food of tsetse-flies (*Glossina swynnertoni* and *G. palpalis*) as determined by the precipitin test.—Bull. ent. Res., **28,** pp. 31–42.

WEITZ, B. (1952). The antigenicity of sera of man and animals in relation to the preparation of specific precipitating antisera.—J. Hyg., Camb., **50,** pp. 275–294.

THE ARTHROPOD POPULATION OF THE SOIL UNDER ELEPHANT GRASS IN UGANDA.

By George Salt

(from the Zoological Laboratory, Cambridge, and the E.A. Agriculture and Forestry Research Organisation, Nairobi.)

Elephant grass (*Pennisetum purpureum*) is the natural vegetation of large areas in the cultivated districts of Uganda, and when shifting agriculture is practised it is often this species that occupies the soil between periods of cultivation. The study of elephant grass is therefore a matter of interest to the Uganda Department of Agriculture, and research on the effects of elephant-grass leys on soil has formed part of the programme of the Agricultural Research Station at Kawanda. In particular, Thomas (1945) has shown the place of elephant grass in the natural distribution of vegetation; Martin (1944, 1946) has demonstrated its beneficial effects in the formation of crumb structure; and Griffith (1949, 1951) has studied the effects of elephant-grass leys on the nitrate content of the soil.

During six weeks spent at Kawanda in the early part of 1949, I was principally engaged in a study of the soil fauna in pastures; but could not avoid feeling that the tradition of the place demanded some attention to elephant grass. Since three or four days' work was required for the collection of the fauna from each sample of soil, it was apparent that no ambitious programme could be completed. My effort was therefore concentrated on one primary object: to provide quantitative information about the arthropod animals inhabiting the soil under elephant grass. It soon appeared that this fauna differs both numerically and in composition from the fauna of cultivated soil and of the soil in adjacent pastures; and the investigation was pressed to the limit of available time in the hope that some of the differences observed may prove to be significant in the special relations that exist between elephant grass and soil.

Methods.

Soil samples were collected by means of a tool which removes a cylinder of soil 4 in. in diameter and 6 in. deep. In the case of the samples to be described here, the tool was re-inserted into the hole and a second core from 6 to 12 in. deep was also removed. It will be convenient to observe that the volume of such a double sample, from the surface to a depth of 12 in., is 150·8 cu. in. (2,471 cc.) and that the area of soil surface removed is 12·6 sq. in. (81·1 sq. cm.). In all cases, surface litter was carefully removed before the sample was taken in order to avoid including in the soil fauna the many animals that merely inhabit the litter on its surface.

The method used for the extraction of the fauna from the samples of soil involved wet sieving, flotation of the biological material in a solution of magnesium sulphate, and separation of the arthropod fauna on a benzene-water interface. A detailed description of the method need not be given here, since two accounts of it have already been published; one as it was originally developed for investigations on wireworms (Salt & Hollick, 1944), the other as it was used in East Africa (Salt, 1952). It is thought to yield all the arthropods (insects, spiders, mites, centipedes, etc.) that are retained by a sieve having a square mesh 0·2 mm. across. What proportion of the tropical soil fauna is too small to be held back by such a sieve is unknown; but it is likely that, as was found in

England, some immature Collembola and many small mites pass through, together with most individuals of a few relatively unimportant groups such as Pauropoda and Protura.

Under the conditions obtaining at Kawanda, three or four days' work was required for the collection and sorting of the fauna from each sample. It was therefore impossible to undertake the examination of more than eight samples in relation to elephant grass. Five of them were handled and examined entirely by myself. The other three, indicated below by the letter K before their number, were partly entrusted to W. Kanakulya, an assistant at Kawanda, who collected them and carried them through the sieving and flotation processes. The organic matter was then put into bottles and preserved in alcohol for subsequent examination. On my return to England, this material was examined without the use of the benzene process, the organic matter being searched for arthropods three or four times. Although the preservation of two samples (K29 and K32) was imperfect, owing to the large amount of vegetable matter they contained, I think all three can be accepted as providing valid information.

Sources of the Material.

Samples of soil were removed from plots on which elephant grass had been growing for one, five, and eight years, respectively, and from a plot under cassava which, in the ordinary scheme of rotation, was to be followed by an elephant-grass ley within the next few weeks. The histories of these four plots are as follows.

First-year elephant grass.—Samples K32 and 33 from Block X Strip 6. This ground was under a standard rotation. In 1945, it had carried sorghum, in 1946, cotton, in 1947, groundnuts interplanted with cassava. The cassava was dug to make way for elephant grass planted in February and March 1948 and the samples were taken on 22nd and 23rd February 1949. Dr. Griffith kindly provided the following information about the soil of this strip: pH, 6·5, percentage moisture at sticky point, 24·6, percentage N, 0·155 (upper), 0·136 (lower sample), nutrients (rapid tests), high P, medium K, medium Ca. Weeds observed in the vicinity of the sampling site were *Sida*, *Cajanus*, *Commelina* and a sedge.

Fifth-year elephant grass.—Samples 30 and 31 from Block VI Strip 5. Elephant grass was planted in this strip early in 1944. At the time of sampling, February 1949, it was about 15 ft. high and formed tangled thickets which could scarcely be penetrated without slashing. Between the thickets were *Sida*, *Cajanus*, *Lantana*, *Panicum maximum* and other weeds.

Eighth-year elephant grass.—Samples 28 and K29 from Block XI. This plot was not under the same rotation as the others and its history before 1941 was not ascertained. Since that year it had been continuously under elephant grass which, at the time of sampling, was only about 12 ft. high and formed untidy thickets with many weeds.

Cassava.—Samples 34 and K35 from Block X Strip 1. This ground was under the same rotation as the plot of first-year elephant grass, but one year behind. It had produced two crops of cotton, in 1945 and 1947, and a crop of sorghum in 1946. In 1948 it had supported groundnuts interplanted with cassava, and at the time of this investigation the cassava was ready for digging and was to be replaced by an elephant-grass ley. Sample 34 was taken on 28th February from a part of the plot where the fully grown cassava provided dense shade over soil that was free of weeds but covered with a slight litter of dead leaves. Sample K35 was collected on 24th January from an area where the cassava cast a less dense shade and where there was a sparse growth of weeds, chiefly blue couch-grass, *Digitaria scalarum*.

Fallow ground.—The two samples examined from under cassava can be eked out by four samples examined in another connection. For the purposes of one of Dr. Griffith's experiments, two adjacent plots had recently been cultivated and left fallow. One plot was exposed naturally to the sun; the other was shaded by brown matting supported at a height of about 4 ft. on a light framework of poles. For our present purpose, these two plots can be accepted as having been at that point in the rotation when a crop has been removed and when elephant grass is about to be planted; that is, at about the same stage as the plot of cassava. Two samples were examined from each plot. A complication is introduced by the fact that these four samples were taken to a depth of only 8 in. but, since by far the larger part of the population occupies the uppermost soil, and since one of these samples was found to contain rodent dung associated with an excessive number of mites, it is probable that the total number of arthropods collected from them would not have been very different if they had been taken to 12 in. depth.

Observations and Comparisons.

The number of individuals of each of the main arthropod groups that was found in each sample is set out in Table I. In the six samples from under elephant grass were found 489, 594, 616, 727, 894 and 919 arthropods, of which six numbers the mean is 706 with standard error 70. In the two samples from under cassava there were 152 and 287 arthropods. On the basis of these eight samples taken for the purpose it appears that the soil under elephant grass had a much larger arthropod population than that under cassava.

Fortunately, the basis of comparison can be broadened by bringing in the four samples from ground that had been recently cultivated and left fallow. The numbers of arthropods found in those samples are set out in the last four columns of Table I, and show total populations of 120, 189, 194 and 330 (mean 208 ± 44). When these samples are admitted to the comparison, we have six samples from cultivated soil at Kawanda to set against the six from elephant grass. The former have a mean arthropod population of 212 ± 33 (representing 26,150 individuals per sq. metre); the latter 706 ± 70 (87,147 per sq. metre). These numbers allow a firm conclusion that the arthropod population of soil under elephant grass is very much larger than that of adjacent and similar soil under cultivation.

The assumption that naturally follows from this conclusion is that the number of arthropods in the soil increases greatly when an elephant-grass ley takes its place in the crop rotation. Further than that, it appears that the increase occurs rather rapidly, since arthropods were already numerous in the samples examined from the plot carrying elephant grass only one year old. It is also to be assumed that most of the arthropod animals living in the soil under elephant grass die when the ground is cultivated to make way for a crop.

That arthropods are less numerous in cultivated than in undisturbed soil is probably a general phenomenon, and it is therefore fortunate that there are other figures with which the population found under elephant grass can be compared. In the course of an investigation of the arthropod population of the soil in some East African pastures there were actually found 442 ± 77 arthropods per sample, representing a population of 54,565 per sq. metre in the uppermost 6 in. of soil. But these numbers make no allowance for two samples which passed directly through ant nests, as shown by the presence of large numbers of eggs, larvae and pupae, and for one sample in which were found 908 mites, probably attracted by the presence of dung. When allowance is made for those abnormal samples, the best estimate is one of 311 ± 20 arthropods per sample, representing a population of 38,417 per sq. metre in the uppermost 6 in. of soil (Salt, 1952, p. 212).

These samples from pasture cannot be immediately compared with those from elephant grass because they were all single samples, taken from the surface to a depth of only 6 in. Three of the double samples from elephant grass, however, were examined in two parts. Sample 28 contained 422 arthropods in the upper and 67 in the lower part; Sample 31 contained 649 and 78, and Sample 33, 709 and 185 in the corresponding parts. In these three samples the upper part, from the surface to a depth of 6 in., contained 84 per cent. of the population. Assuming the same distribution of the fauna in the other three samples, we can calculate the arthropod population under elephant grass to be 596 per single sample, or 73,517 per sq. metre in the top 6 in. of soil. This is considerably larger than the gross population found in the undisturbed soil of grazed pastures, and nearly twice as large as the corrected estimate of the population from that source.

TABLE I.

Arthropods collected from soil samples from elephant-grass leys and cultivated ground at Kawanda, Uganda.

	Elephant grass						Cultivated ground					
	1-year		5-year		8-year		under cassava		in shade		in sun	
Sample number	K32	33	30	31	28	K29	34	K35	36	38	37	39
Collembola ..	370	538	183	195	124	52	94	7	23	19	16	35
Thysanura ..	2	4	—	19	—	3	—	—	—	—	—	—
Orthoptera ..	—	—	2	2	1	—	1	—	—	—	—	—
Isoptera ..	3	9	5	66	4	12	1	—	—	5	20	—
Psocoptera ..	1	—	—	—	1	1	2	—	1	1	—	—
Thysanoptera ..	1	—	11	1	1	1	—	—	—	—	1	—
Hemiptera ..	57	22	7	57	18	104	4	—	—	2	1	5
,, (Aphids) ..	—	2	—	1	10	35	—	—	—	—	—	—
Coleoptera ..	—	2	55	11	1	7	—	—	1	1	—	—
,, (larvae)	5	102	4	28	26	15	16	11	16	9	46	24
Lepidoptera ..	—	2	—	—	—	2	5	—	—	—	—	—
Diptera	34	1	8	28	22	54	23	—	3	—	4	2
Hymenoptera ..	2	3	1	2	2	—	—	1	—	—	—	—
,, (ants) ..	13	20	221	14	99	117	15	3	—	—	—	—
Acarina	94	91	405	248	140	153	115	125	52	283	99	112
Araneida ..	6	5	5	8	3	2	3	1	1	—	—	—
Chilopoda ..	1	3	9	5	2	20	1	1	2	1	2	—
Diplopoda ..	—	—	—	1	—	—	—	—	—	—	2	—
Palpigradi ..	12	9	2	2	1	6	—	—	3	4	1	6
Pauropoda ..	2	1	—	—	—	—	1	—	7	3	1	—
Symphyla ..	10	76	—	29	27	2	6	—	10	2	1	5
Total Insecta ..	488	705	497	424	309	403	161	22	44	37	88	66
Total Arachnida	125	185	421	293	173	183	126	127	75	293	106	123
Unclassified ..	3	4	1	10	7	8	0	3	1	0	0	0
Total Arthropoda	616	894	919	727	489	594	287	152	120	330	194	189

For size of each sample, see p. 539.

The scanty information at present available on the fauna of the soil in tropical regions other than East Africa has recently been reviewed (Salt, 1952). No population as dense as that found in the soil of East African pastures had previously been reported. The arthropod population under elephant grass, therefore, is much larger than, indeed nearly twice as large as, any other population yet known from tropical soil. Nevertheless, it is still not as large as the population of 732 ± 64 arthropods per sample (90,238 per sq. metre in the top 6 in.) that was found by exactly the same method of examination in twenty-five samples from an English pasture.

It is a matter for regret that the number of samples examined is too small to allow any trustworthy comparison to be made between the composition of the arthropod population under elephant grass and that under pasture or in cultivated soil. In the six double samples from elephant grass, for instance, 34·5 per cent. of the individuals collected were Collembola. This is very similar to the 35·9 per cent. of Collembola found by the same methods in twenty-five double samples from English pasture (Salt & others, 1948), and markedly different from the 38 228
12·0 per cent. of Collembola in eleven single samples from East African pastures (Salt, 1952). But, as can be seen in Table I, Collembola were especially numerous in the two samples from first-year elephant grass, and made up only 20·3 per cent. of the fauna collected from the other four samples. It is clear that quantitative conclusions cannot be based on analysis of the details of so few samples, and it remains merely an impression that the soil under elephant grass differed from other soil examined in East Africa not only in the number but also in the kinds of arthropods it contained.

Discussion.

The foregoing observations bear on two subjects that have been studied in connection with elephant grass: the crumb structure of the soil and the availability of nitrogen after elephant-grass leys.

Crumb structure.—Most of the smaller soil arthropods do not maintain burrows, and are entirely dependent for living-space on the presence of small crevices in which they can breathe and move about. In those soils whose texture affords only minute pore-spaces, a good soil structure predisposes to an increased population of soil arthropods because it provides crevices large enough for them to live in. The work of Martin (1944) has demonstrated the formation of a crumb structure under elephant grass; and evidence of its presence in the soil examined in the present investigation was provided by the difficulty experienced in washing all six elephant-grass samples, but none of those from cassava or fallow ground, through the middle sieve (2·5 mm. square mesh) of the apparatus. This crumb structure is probably one of the factors that explain the large population of soil arthropods found in elephant-grass leys as compared with the much smaller numbers found in cultivated soil.

If the living-space provided by crumb structure is invoked to explain the larger arthropod population under elephant grass, it must be considered that crumb structure is also developed under other grasses, including *Cynodon*, *Chloris* and other pasture forms (Martin, 1946). The arthropod population found under these and other grasses in East African pastures was considerably lower than that found under elephant grass. The difference is probably to be explained by insolation. The surface of grazed pastures in East Africa is frequently exposed to strong solar radiation which produces high temperatures and extreme dryness in the superficial layers of soil. Both of these conditions are inimical to most soil arthropods, and it is probably owing to limitations they impose that the fauna of pasture soils is so much less numerous in East Africa than it is in England (Salt, 1952). Against both conditions, elephant grass provides protection. Not only do the giant culms shade the ground from much radiation, they also conserve and even contribute to a high humidity at the surface by hindering air movements and by transpiration. For these reasons the soil under elephant grass might be expected, as it was found, to contain larger populations than that of strongly insolated pastures.

There is also the possibility that the large number of soil arthropods under elephant grass is not merely a consequence of the crumb structure but also in part the cause of it. A considerable body of information has accumulated (Anon., 1948) about the effect of organisms of various kinds, but especially earthworms, on soil structure. Earthworms were notably scarce in the soils examined in East Africa, but the number of arthropods found under elephant grass, 596 per single sample, represents a population of 7·9 per cu. in. in the top 6 in. of soil. Most of these animals are very small; but when they are present in such numbers, their movements, respiration, digestion and excretion must be expected to have in time a considerable influence on the structure and chemistry of the soil.

Availability of nitrogen.—Working at Kawanda, Griffith (1949, 1951) has shown that after an elephant-grass ley is cultivated there is (1) a gradual increase in the nitrate content of the soil, (2) a delay of several weeks or months before this nitrogen becomes fully available, and (3) a correlation between the increase in nitrate and the incidence of rainfall. Considering in relation to these observations (1) that the arthropod population found under elephant grass shows an excess of 60,000 per sq. metre over that found in cultivated soil, (2) that the nitrogen contained in the tissues of these animals, particularly that in the chitin and sclerotin of their exoskeletons, would not be in a state available to plants for several weeks or months after their death, and (3) that the freeing of the nitrogen locked up in these exoskeletons would be accelerated by wet conditions, an investigation is called for, to see whether these parallel facts may be connected.

Unfortunately no direct measurements of the nitrogen contained in the arthropods collected under elephant grass can be given, because the collections have been broken up and distributed to specialists. In any case the whole animals, which alone were collected and counted, would not have been sufficient for this problem. The use of a benzene-water interface as a means of separating arthropods from other organic material reveals the presence in soil of a considerable amount of arthropod cuticle from dead individuals which are not included in the census of the population. Head-capsules, legs, elytra, abdominal sclerites, shells of Oribatid mites and fragments of exoskeleton of all sorts are numerous in soil, but are naturally not taken into account in the few estimates of arthropod biomass that have yet been made. The chitin and tanned protein of which these fragments are composed contains about 10 per cent. of nitrogen.

The substances that compose the arthropod cuticle are extremely resistant to decomposition. Under dry conditions, for instance in museum cabinets, insect exoskeletons have remained undecomposed for two centuries; even in soil they are very persistent, as is shown by the fragments mentioned in the preceding paragraph. There is no doubt, moreover, that they persist much longer in dry soil than in wet. Nitrogen locked up in these tough substances can therefore be assumed to accumulate in the surface soil during a dry season and to be liberated by their decomposition at the onset of rains.

These considerations suggest that there is an *a priori* case for an investigation of the soil arthropods as a repository of nitrogen under elephant grass, and as a source of some of the nitrate gradually released in the first year of cultivation.

Summary.

Six soil samples from elephant-grass leys at Kawanda, Uganda, gave collections representing a population of 87,147 arthropods per sq. metre in the top 12 in. of soil.

Six samples from adjacent cultivated ground gave collections representing a population of 26,150 arthropods per sq. metre.

These numbers are compared with the population of arthropods found in the soil of grazed pastures in East Africa.

The greater population under elephant grass is attributed to the presence of a crumb structure and to the protection afforded by elephant grass against insolation.

It is suggested that the nitrogen contained in these soil arthropods, especially that locked up in the chitin and sclerotin of their skeletons, is part of the nitrate that becomes available some weeks or months after elephant-grass leys are cultivated.

Acknowledgements.

I should like to express my thanks to Dr. G. ap Griffith and Mr. E. A. B. Williams for the friendly way in which they furthered my work at Kawanda, to W. Kanakulya for his assistance, and to Dr. M. G. M. Pryor for a helpful discussion about arthropod exoskeletons. Grateful acknowledgement is made to the Colonial Office for establishing the Research Scheme that made this work possible and to Sir Bernard Keen, F.R.S., for so kindly and efficiently administering it.

References.

Anon. (1948). Soils & Fert., **11,** pp. 1–5.

Griffith, G. ap (1949). E. Afr. agric. J., **14,** pp. 187–188.

Griffith, G. ap (1951). Emp. J. exp. Agric., **19,** pp. 1–2.

Martin, W. S. (1944). E. Afr. agric. J., **9,** pp. 189–195.

Martin, W. S. (1946). Rep. Dep. Agric. Uganda, 1944–45, pt. 2, pp. 10–24.

Salt, G. (1952). Bull. ent. Res., **43,** pp. 203–220.

Salt, G. & Hollick, F. S. J. (1944). Ann. appl. Biol., **31,** pp. 52–64.

Salt, G., Hollick, F. S. J., Raw, F. & Brian, M. V. (1948). J. Anim. Ecol., **17,** pp. 139–150.

Thomas, A. S. (1945). J. Ecol., **33,** pp. 10–43.

STUDIES ON AQUEOUS SUSPENSIONS OF INSECTICIDES.

PART V. THE SORPTION OF INSECTICIDES BY SOILS.

By F. Barlow and A. B. Hadaway
Colonial Insecticides Research Unit, Porton.

J -
A - T.

Previous work (Hadaway & Barlow, 1952) has shown that solid particles of insecticides deposited from aqueous suspensions could disappear very rapidly from the external surfaces of blocks made of some tropical soils. This physical process was thought to be one of adsorption and involved complete loss of biological activity of those compounds, such as DDT and dieldrin, which possess little or no fumigant action. On the other hand, it extended the effective life of fumigants such as γ BHC and aldrin. This paper collects together some miscellaneous items of work on this phenomenon.

The Sorption Process.

Experiments described by Hadaway & Barlow (1952), in which particles of γ BHC were moved away from the surface of the mud blocks, clearly showed that the sorption of this insecticide by the mud was from the vapour phase and loss was not due to a migration of molecules from the solid over the surface of the sorbent. As the rates of sorption of particles of DDT, aldrin and dieldrin of the same size, compared with γ BHC, were approximately in the ratio of their vapour pressures, these compounds are also presumably adsorbed by mud from the vapour phase.

If the disappearance of insecticides from lateritic mud surfaces is due to adsorption it should also happen on other adsorbents. It was not easy to see if this was so on aluminium oxide or silica gel because insecticide particles were difficult to observe on these materials. Charcoal, being black in colour, enabled particles on its surface to be readily seen and, on blocks of respirator charcoal, DDT disappeared at about the same rate as it did on Uganda mud. This provides an illustration of the high sorptive power that the lateritic soils possess. Activated iron oxide gels prepared as described by Lambert & Clark (1927) were even more effective than charcoal. Crystals of DDT less than 10 microns in size were sorbed in about two hours as compared with two to three days, 10–20 micron particles of γ BHC in about one hour compared with overnight, while a flat plate of aldrin, 10 by 30 microns, lying flat on the surface, disappeared in about ten minutes. It is of great interest that iron oxide can be so active in a physical sense because the most active soils, the laterites, contain high proportions of this substance.

The highest rates of sorption were obtained when the insecticide particles were in close contact with the sorbent. Movement away from the surface greatly reduced the rate. This was so even if the distance was only the width of a few particles, for if particles were piled on top of one another the bottom ones were sorbed first. Also, if single crystals were observed microscopically, it was obvious that the molecules were not being removed from all over the crystals but from the side next to the sorbent. The crystals became thinner and thinner and before finally disappearing were just ghost-like outlines of their original selves. Thus the forces which cause the rapid transfer of molecules from the solid are only of short range.

Normally such compounds as DDT evaporate very slowly. At room temperature, DDT has a life of considerably more than a year on many surfaces, yet on lateritic mud the same particles will disappear in a few days. Evidently the rapid removal of vapour molecules from a DDT surface by adsorption greatly accelerates the rate of evaporation at that surface. The accommodation coefficient of DDT is said to be very low (Kuhn & Massini, 1949), and presumably therefore the evaporation coefficient is also much less than 1 and the evaporation rate will be much less than would be expected from its vapour pressure. If the DDT-laterite system behaves like a molecular still, for example, and the evaporation coefficient is increased by sorption to about 1, then the rate of evaporation should correspond to the Knudsen rate, or the rate measured by an effusion method (*cf.* Hickman & Trevoy, 1952).

Some figures for the evaporation rates of DDT measured by an effusion method have been provided by Messrs. J. Hyman & Co. At 28°C. the evaporation rate is $2{\cdot}75 \times 10^{-9}$ gm./cm.^{2}/sec. If it is assumed that all evaporation proceeds from the side of the particle next to the sorbent, and that particle size corresponds to the thickness of the particles, *i.e.*, a 5 micron particle is 5 microns thick in the direction away from the surface, it is possible to calculate roughly the residual life of DDT particles resting on mud surfaces. The calculated and the observed life of DDT particles are given in Table I, and agreement is reasonably good considering the assumption made and that ranges of particle size were used in the experimental work.

TABLE I.

Comparison of calculated and observed life of particles of DDT resting on mud surfaces.

Calculated life in days for particles at mid-point of range.		Observed life in days at a dosage of 25 mg. per sq. ft.	
5μ	3·2	0–10μ	2–3
15μ	9·6	10–20μ	5
30μ	19·3	20–40μ	14

The short-range adsorptive forces probably also give an explanation of some observations on the lives of particles of γ BHC of different sizes which were presented in a previous paper (Hadaway & Barlow, 1952). Immediately after spraying, the efficiency of each range of particle size was inversely proportional to its size. As the smaller particles disappeared from the surface, the blocks which had been treated with them became less efficient as compared with those treated with larger sizes, because they now depended on fumigant action alone. Therefore, for a time, efficiency was directly proportional to particle size. This, of course, was to be expected as larger particles have a longer residual life than smaller ones. However, when the particles of larger size range finally disappeared, and all treated blocks depended only upon fumigant action, the relative efficiencies reverted almost to their original sequence. There are two possible reasons for this. The larger particles can lose a larger percentage of their mass by direct evaporation to the atmosphere because they have longer lives and therefore the eventual concentration of γ BHC adsorbed on the mud will be less from larger than from smaller particles. Another reason is that, for a given weight of deposit, larger particles cover a smaller area of mud surface than do smaller ones. If the adsorptive forces are only of short range the insecticide vapour will be sorbed only over a small area in the neighbourhood of each individual large particle, areas farther from the crystals will not receive any vapour.

Therefore, when all the crystals have disappeared, there will be a smaller area of surface from which γ BHC is being desorbed on the blocks treated with larger crystals than on those treated with smaller ones.

Adsorption usually decreases with increasing temperature but in the present instance this is not so for the following reasons. Gases and vapours are adsorbed rapidly, and therefore the limiting factor in the sorption rate of solid insecticide particles will be the evaporation rate of the vapours from the solid. This will increase with temperature and, as the weight of insecticide compared with the weight of sorbent is very small, any decrease in the rate and magnitude of sorption will not be important. The approximate life of DDT particles on Uganda mud blocks at different temperatures is given in Table II.

TABLE II.

Mud blocks sprayed with 0–10 micron DDT suspension at 100 mg. per sq. ft.

Temperature (°C.)	25	30	40	50
Approximate life in hours ..	72	48	8–10	4–5

This adsorption of insecticide particles lying on a block of compacted adsorbent is obviously a difficult one to investigate experimentally in order to obtain quantitative physical measurements. The weight of insecticide is very small compared with the weight of sorbent, as mentioned above. The distribution of the particles on the mud surface is a function of the spraying apparatus used and an absolutely uniform mono-particulate layer can never be obtained. In addition, the particles should be all of the same size. A further difficulty is that the external surface of the mud blocks should be quite smooth, permitting uniform contact over the surface which the particle presents to the block. This again is an ideal not obtainable in practice. Uganda mud blocks are relatively smooth but even they give all degrees of contact to particles lying on their surfaces. Other soils are far worse and may have large pieces of inactive constituents mixed with active ones.

From this it can be seen that the investigations that can be made on the actual sorption process are few and qualitative. Once DDT has been completely sorbed it is in a more amenable condition.

Diffusion of DDT within the Block.

After sorption is completed, the DDT is situated on the internal surface of the mud block, decreasing in concentration rapidly in the direction at right angles to the sprayed external surface. It is possible to follow the subsequent fate of the DDT because little is lost by desorption, which is a very slow process. By sectioning the blocks at different time intervals it was possible to show that the sorbed DDT diffused slowly inwards away from the sprayed surface.

The method employed was to spray duplicate Uganda mud blocks with 0–10 micron DDT particles at a dosage of about 100 mg. per sq. ft. The blocks were kept at 25°C. and sampled by removing layers of known thickness, extracting each layer with benzene and determining the DDT colorimetrically as described by Hadaway & Barlow (1952). The results shown in Table III are smoothed values taken from experimental curves. Total recoveries of DDT in mg. per sq. ft. after 2 weeks, 3 months, 6 months and 12 months were 119, 100, 92 and 114, respectively.

This experiment also provided further evidence that decomposition is of no importance in the inactivation of DDT on these muds. Even after 12 months in the adsorbed state the recovered DDT had suffered negligible decomposition.

This is shown both by the high total recovery and by a comparison of the absorption curves of the nitrated derivatives used in the colorimetric determination of DDT. The absorption values in terms of readings on a Spekker absorptiometer for 32 μg. of p,p′ DDT, 32 μg. of ethylene derivative and for a sample containing the same amount of DDT extracted from a layer of a mud block 12 months after spraying are given in Table IV. The absorption curves were determined by means of Ilford spectrum filters.

TABLE III.

Accumulative percentage recovery of p,p′ DDT at different distances through mud blocks.

Time after application	Distance through block in cm.											
	0·1	0·2	0·3	0·4	0·5	0·6	0·7	0·8	0·9	1·0	1·1	1·2
2 weeks	80	96	100									
3 months	33	60	78	89	97	100						
6 months	16	30	43	54	64	73	80	87	93	100		
12 months	10	21	32	41	51	60	67	74	81	87	93	100

This slow diffusion inwards has an analytical consequence. Deposits of DDT on walls are often sampled by scraping away the superficial layer of wall surface to a depth of say 0·5 to 1, 2 or even 3 mm. and analysing these scrapings. It can be seen that, apart from showing DDT present which may not be available biologically because of sorption, the method will also show a progressive decrease in DDT content of similar scrapings with time. This has been observed, for instance, in India and put down to decomposition or abrasion of the DDT (Pal & Sharma, 1952; Viswanathan, 1952). It could, at least partially, be due to diffusion inwards.

TABLE IV.

Absorption values of the coloured products formed in the colorimetric method of analysis for DDT.

Sample	Filter numbers (with absorption maxima in brackets)			
	604 (520)	605 (550)	606 (580)	607 (600)
p,p′ DDT	·095	·135	·175	·160
DDT recovered from mud ..	·110	·140	·175	·156
p,p′ ethylene DDT	·165	·129	·053	·010

It has been mentioned above that desorption is a very slow process. For example, γ BHC, which is sorbed in a few hours, requires several months for desorption, the rate of loss decreasing all the time. DDT, as particles less than 10 microns in size, which disappear in two to three days, shows negligible desorption after 12 months. This slow desorption rate is to be expected as it would be more akin to the natural evaporation rate which, in the case of DDT, is of the order of years at normal room temperatures. It should be less than the evaporation rate of crystals lying in the open air, as the vapour molecules have to move through narrow capillaries by diffusion, and there is no mass movement of air to aid them. Furthermore, the diffusion of sorbed insecticide deeper into the sorbent will, of course, oppose desorption.

A Laboratory Test for Sorptive Properties of Soils.

The most straightforward estimation of the capacity of a soil to inactivate DDT and other insecticides is to spray it, in block form, with a suspension of pure insecticide particles and observe any decrease or disappearance of the deposit. This is difficult on some soils and also requires the preparation of a pure insecticide suspension without the inert diluents which are found in commercial wettable powders.

Downs & others (1951) have used the capacity of soils to decompose DDT at 130°C. in order to test for inactivation properties, but this is measuring a chemical property of the soil under conditions very different from those at which the physical process of adsorption occurs. The decomposition is catalysed by iron oxides which also seem to be the effective adsorbents, particularly of such soils as laterites, but whether this correlation is applicable in general would have to be decided by tests on many samples of different origin.

It is therefore desirable to find a test which depends more directly upon adsorptive properties. As ability to sorb insecticides seems to go with general adsorptive properties, adsorption isotherms of more permanent gases and vapours could be measured, but such figures cannot be obtained easily under field conditions. A simpler procedure is to find, by weighing, the amount of a vapour such as carbon tetrachloride which can be taken up at the saturated vapour pressure at a given temperature. This could easily be done as a field test needing only simple equipment. Carbon tetrachloride was chosen because it is a non-polar compound akin to the chlorinated hydrocarbon insecticides.

In fact, this type of test proved to be only of limited application in that, although highly active soils showed correlation between carbon tetrachloride and insecticide adsorption, less active ones did not. If a given soil can sorb between about 20 and 30 per cent. of its weight of carbon tetrachloride then it will probably be unsuitable as a substrate for residual insecticides such as DDT. If it sorbs about 15 per cent. or less it may or may not have some sorbent action for insecticides. The very variable chemical and physical nature of the less active soils renders a simple correlation unlikely.

In order to obtain reproducible results some precautions are necessary. The block of soil must be freed from water which it normally contains in equilibrium with the water vapour in the atmosphere, and the temperature during the estimation must be constant. The test was, therefore, performed as follows: the soil was passed through a 40 mesh sieve and mixed with sufficient water to give a thick plastic mass and then pressed into cylindrical metal rings, 2·3 cm. diameter and 1·2 cm. deep. After drying at room temperature, the rings were removed to yield small blocks of soil. A block was placed in a desiccator over concentrated sulphuric acid for 24 hours and weighed. It was then placed in a desiccator over carbon tetrachloride for a further 24 hours and reweighed. An investigation of the rate of sorption showed that there was little increase in weight after 24 hours. The temperature of the desiccators was kept at 25°C. throughout. Some results for a selection of soils are shown in Table V, and results with other soils are given in the next section.

If benzene was used instead of carbon tetrachloride, about the same volume was sorbed and different soils appeared in the same sequence. Water vapour was not suitable because the rate of sorption at the saturated vapour pressure was very slow, and values comparable to those obtained with carbon tetrachloride and benzene were not arrived at even after 10 days.

TABLE V.

Percentage by weight of carbon tetrachloride vapour sorbed by some tropical soils.

Jamaica (red)	Uganda	Nigeria	Jamaica (grey)	Kenya	India
29	24	19	13	5	3

The Sorptive Properties of Different Soils.

Samples of soils were obtained from the United Kingdom and from different parts of the world. Each soil was mixed with water and made into small blocks as described above. Blocks of each soil were either sprayed with 100 mg. per sq. ft. of 0–10 micron DDT particles or were tested for sorption of carbon tetrachloride. The duration of life of the DDT deposits was determined visually with the sprayed blocks kept at 25°C. The results are given in Table VI.

The samples of Mexican soils were those used by Downs & others (1951) and we can confirm that it is the red soil with high iron oxide content which is by far the most active although not as much as some of our other samples of red soils. The grey Mexican soil has a relatively high carbon tetrachloride sorption but this is in the range where correlation is not good.

TABLE VI.

The residual life of 0–10 micron DDT particles on different soils.

Origin of soil	Approximate time to disappearance in days	Percentage carbon tetrachloride sorbed in 24 hours
Uganda, red	3	25
Lagos, red	3	19
Jamaica, red	3	29
Taveta, Kenya, grey ..	4	22
Mexico, red	10	18
Taveta, Kenya, red ..	10–14	5
Jamaica, grey ..	8	13
India, grey	20	3
Weald clay (U.K.) ..	10–11	9
Liberia, grey	20–25	11
Upton (U.K.)	No change in 3 months	2
Evesham (U.K.) ..	,,	5
Wantage (U.K.) ..	,,	3
Martock (U.K.) ..	,,	6
Bridgnorth (U.K.) ..	,,	2
Worcester (U.K.) ..	,,	7
Acid peat (U.K.) ..	,,	9
Mexico, grey	,,	13
Mexico, brown ..	,,	5

Apart from the Weald clay, all the U.K. soils tested were inactive. The very active soils were the tropical lateritic ones, in sorbing both DDT and carbon tetrachloride. They were generally red in colour, an exception being the grey soil from Taveta. Other soils from tropical countries were less efficient than the laterites but did show some action. It should be noticed that in these tests the smallest DDT particles were used in order to obtain results as quickly as possible. They, of course, have the shortest life and normal wettable powders with larger particles would remain for a longer period, particularly on the less active soils and at higher dosages than 100 mg. per sq. ft.

Any conclusions made can only be rough generalisations as there are always exceptions. One noticeable exception was given by the Taveta red soil. This had a reddish brown appearance but was obviously different in texture from the other laterites. It contained a proportion of larger, hard, quartz-like fragments and it was noticeable that particles of DDT which rested on these lasted for a much longer time than on the neighbouring surface. This may explain to some extent the longer residual life of DDT deposits on this Taveta mud. However, the Taveta mud was different in other ways. It contained a high proportion of iron oxide but this cannot have been as active as it was in other laterites. The carbon tetrachloride sorption was low and hardly changed even when the blocks consisted of 50 per cent. gravel. (If Uganda mud is mixed with inert material the carbon tetrachloride figure is in proportion to the percentage of mud used). The laterites adsorbed water vapour only slowly and only reached equilibrium after several days. Taveta mud sorbed rapidly at first but almost the maximum amount of water was taken up in 24 hours.

TABLE VII.

The sorption of water vapour by two soil samples.
Percentage by weight of water sorbed at different times.

	No. of days					
	1	2	4	6	8	10
Taveta mud ..	5	6	6			
Uganda mud ..	5	7	9	11	12	14

Thus, although the mud from Taveta on general appearance seemed to be in the same class as the other laterites and actually did adsorb DDT, although rather slowly, it had many different properties. Davidson (1953) has carried out tests with experimental huts at Taveta and did not find any marked evidence that sorption of insecticides was occurring. One partial reason for this may be that the Taveta mud is not a particularly active one compared with the Uganda samples. The possession of a reddish-brown colour and a high iron content does not always indicate adsorptive properties for insecticides although in three out of four samples tested it has done so.

Some tests were made on the effect of diluting an active soil with an inert material such as is often done by the builders of houses. Uganda mud was mixed with 25 and 50 per cent. of sand and made into blocks. This incorporation of sand had no observable effect on the residual life of DDT particles sprayed on to the surfaces of these blocks. Presumably the sand particles were sufficiently closely surrounded with, and covered by, particles of mud to permit a reasonably close contact between DDT and mud.

Attempts to Prevent Sorption.

(a) The simplest and most direct method of preventing sorption would be to block the capillaries of the sorbent with a colloidal material which dries to an impermeable film. To do this most effectively would require pretreatment of the walls, an expensive and laborious process to be avoided if possible, and in addition would render the wall surface non-absorbent. We have shown previously that deposits from wettable powders on non-absorbent surfaces are much less effective than on absorbent ones and therefore sorption could only be prevented at the price of having a less efficient deposit. A short experiment on pretreatment was performed in order to show this effect. Uganda mud blocks were painted with a 2 per cent. solution of size in water and allowed to dry for 4 days in room temperature. They, and untreated blocks, were then sprayed with a suspension of DDT. Mosquitos were exposed to some blocks a few hours later, and to other blocks 15 days later. The results are given in Table VIII, and it can be seen that blocking the capillaries prevents sorption but reduces the availability of the DDT particles.

TABLE VIII.

Mud blocks sprayed with 0–10 micron DDT at 100 mg. per sq. ft.
Blood-fed female *Aëdes aegypti*, 2–3 days old, exposed for short contact periods.

	Days after spraying	Mean percentage kill 24 hours after exposure of. . . min.								
		0·25	0·5	1	2	4	8	16	32	64
Pretreated . .	0				20	45	88			
	15				18	45	76			
Untreated . .	0	100								
	15								8	21

Biological tests were not made with higher concentrations of size because visual inspection showed that with 5 and 10 per cent. solutions the DDT particles were very firmly stuck to the surface.

(b) Maes (1952) has reported that pretreatment with phosphate solutions can prevent or reduce the rate of decomposition of DDT residues on walls. Although we know that sorption occurs without decomposition it was thought that phosphates might possibly stop the loss of effectiveness of DDT on lateritic mud by some precipitation reaction or by some effect on the adsorbent iron oxide. Therefore, Uganda mud blocks were heavily sprayed with molar dipotassium hydrogen phosphate solution or with solutions of some complex-forming and precipitate-forming reagents for ferric ions. These were 5 per cent. of the disodium salt of ethylene diamine tetracetic acid, 10 per cent. potassium ferrocyanide, 10 per cent. sodium dimethyl dithiocarbamate, and 5 per cent. Cupferron solutions. Some blocks were also treated with a 10 per cent. solution of calcium chloride to see if the presence of a deliquescent solid could have any effect by keeping the surface wet. After being left for 24 hours to dry, the blocks were sprayed with 0–10 micron DDT particles at a dosage of 100 mg. per sq. ft. and observed visually while kept at 25°C. There was no detectable effect on the sorption rate of DDT on Uganda mud.

(c) Another possible way of preventing sorption would be to find a " poison " which would be rapidly and preferentially adsorbed on to the mud. It should be chemi-sorbed so that it would not subsequently desorb and permit the normal insecticide sorption to proceed. Dr. Maxted in correspondence has informed us that poisoning does not occur on oxide catalysts and therefore this does not seem to be a possible way of preventing the sorption of solid insecticides on mud walls.

(d) Insecticidal coatings based on urea-formaldehyde resins have been considered to be suitable for application to dried mud. The residual action of these formulations was therefore studied by applying 50:50 urea-formaldehyde alkyd resins containing 10 per cent. DDT or 5 per cent. dieldrin to dried Uganda mud blocks and to glass plates. When the resin films had dried they could be peeled off and had obviously penetrated only very slightly into the mud. Twenty hours after application, the films containing DDT were lifted from each surface and analysed. Those from glass plates contained an average of 10·2 per cent. DDT, whereas those from mud had an average of 3·6 per cent. DDT. Presumably the resin solvents and the insecticide they contained had penetrated further into the mud than had the resins themselves. Kills of *Aëdes aegypti* (L.) exposed in contact with one-day-old films containing nominally 5 per cent. dieldrin on mud blocks were equivalent to those obtained with a concentration of 2 per cent. dieldrin on glass plates. Therefore, concentrations of 10 per cent. DDT and 5 per cent. dieldrin were reduced initially by about 60 to 70 per cent. when applied to mud.

Evidence of subsequent adsorption of insecticide from the films on mud has been obtained in biological and chemical tests with films stored at 25°C. Kills of *A. aegypti* in contact with dieldrin films on mud blocks decreased as the films aged, whereas those of mosquitos in contact with films on glass plates showed no significant change (see Table IX).

TABLE IX.

Aëdes aegypti exposed in contact with 50:50 urea-formaldehyde alkyd resin films containing 5 per cent. dieldrin.

Surface	Age of film	Mean percentage kill after exposure of. . .min.				
		4	8	16	32	64
Glass	1 day	13	58	98		
	2 weeks	10	63	98		
	4 weeks	10	70	98		
	6 weeks	—	65	95		
Uganda mud blocks	1 day		3	53	95	
	2 weeks		0	15	78	
	4 weeks		0	0	53	
	6 weeks			0	0	0

Similarly, analysis of the urea-formaldehyde films on mud after seven weeks gave a DDT content of 0·6 per cent. compared with 3·6 per cent. one day after application. DDT was also determined in successive layers of mud removed from the blocks. The first layer weighed 0·50 gm. and consisted of the urea-formaldehyde film together with about 0·2 mm. of mud. Each subsequent layer weighed 2·0 gm. and was about 0·8 mm. thick. The figures given in Table X are the weights of DDT in microgrammes recovered from each layer.

Thus, two separate processes operate to reduce the toxicity of insecticidal resin films applied to an active mud. Initially there is a reduction in the concentration of insecticide in the resin film due to penetration of some of the insecticide with resin solvents into the mud, and this is followed by adsorption of the insecticide from the resin film into the mud. The rate of adsorption of DDT in resin films is slower than that of DDT crystals applied as suspensions because the insecticide has to diffuse from the resin before it can respond to the sorptive forces of the mud.

TABLE X.

Weights of DDT (microgrammes) recovered in successive layers from mud blocks treated with urea-formaldehyde resins containing 10 per cent. DDT.

Time after application	Layer number							
	1	2	3	4	5	6	7	8
1 day ..	2,470	860	90	0				
7 weeks	670	940	550	385	230	162	105	77

Discussion.

There is little doubt that DDT wettable powders can rapidly lose their effectiveness after being sprayed on to walls made of certain air-dried mud and soils. This rapid loss is to be distinguished from relatively slow disappearance spread over months or years and which may be due to everyday agencies such as abrasions, smoke and dirt deposition, evaporation, etc. There are three main points of interest: the nature of the process by which activity is lost, how the loss can be predicted, before spraying schemes commence, by examination of local soils used for building purposes, and how the loss can be avoided by some method of treatment of the walls.

While there have been several reports on the loss of activity of insecticide residues on mud walls, only those by Downs & others (1951), Bordas & others (1953), Pal & Sharma (1952), Viswanathan (1952), and Hadaway & Barlow (1951, 1952) have explored the phenomenon in any detail. All these authors agree that the loss can be very rapid as compared with the expected residual life of DDT and that it occurs most readily on soils of high iron oxide content but there is a difference in stress as to the particular method by which inactivation occurs.

As explained in this and previous papers (Hadaway & Barlow, 1951, 1952), our conclusions have been that the loss occurs by a physical mechanism, adsorption. The evidence for this is as follows. It is general for the insecticides examined and is not restricted to those of one particular group with similar chemical properties; the rates of loss of different insecticides from the surface of an active mud are proportional to their vapour pressures and therefore approximately to their evaporation rates, nor is the loss of a given insecticide restricted to one adsorbent, as it occurs on charcoal, for instance, and is not restricted to materials containing iron oxide; finally, the insecticide can be recovered quantitatively from the soil block after adsorption is complete.

Downs & others (1951), as a result of their first experiments, were of the opinion that DDT was inactivated by a decomposition catalysed by the iron oxides in their soil samples. They showed, by using the method of Fleck & Haller (1944), that the capacity of a series of soils to inactivate DDT at room temperature was proportional to their efficiency in catalysing the decomposition of DDT at 130°C. However, they did not provide any evidence that DDT is decomposed at room temperature when sprayed as a wettable powder on to active soils.

Later, Downs (in Bordas, Downs and Navarro, 1953) agreed that a physical loss of the insecticide is the first step in loss of activity but still continued to stress the occurrence of catalytic decomposition. They say "The phenomenon is found to be due to adsorption of the DDT crystals present on the surface; the adsorption appears to be the initial step in the catalytic decomposition of DDT by iron oxides present in soils, since there is a direct relationship between the amount of oxides present and their capacity to inactivate DDT deposits". Similarly, Pal & Sharma (1952) concluded that both sorption and subsequent decomposition occur because they recovered DDT in surface scrapings when there was no biological activity and because the DDT recovered decreased in quantity with time.

Once it is agreed that adsorption is the actual cause of loss of biological activity, and it is difficult to see how any other mechanism could transport the insecticide from the form of solid particles outside the mud to intimate contact with the catalytically active iron oxides, any subsequent decomposition reactions are only of theoretical interest. It is worth while, however, mentioning a few reasons why decomposition of DDT after adsorption is unlikely or at least, not proven.

Demonstration of the appearance of decomposition products or the quantitative recovery of the DDT applied would be positive evidence as to whether or not decomposition is taking place. Downs & others (1951) have not given any results which demonstrate decomposition at ordinary temperatures. In fact, they say that where there was a loss of insecticidal action within a year after spraying they could recover from 60 to 90 per cent. of the original amount sprayed. Pal & Sharma attribute their declining recoveries to decomposition but this is negative evidence. One would expect the catalytic decomposition product of DDT, the ethylene derivative, to show its presence by a red colour in the Alessandrini method of analysis used by Pal & Sharma but they do not mention that this occurred. On the other hand, we have been able to recover quantitatively p,p′ DDT from Uganda red soil both a few weeks and 12 months after sorption was complete. Any decomposition must have been negligible. The Alessandrini method is not suitable for accurate quantitative work, being intended as a rough field method, and Pal & Sharma say that there are considerable variations, particularly under field conditions. Even in a laboratory test, recoveries varied from 30 to 70 per cent. In further laboratory tests, they could only recover about 50 to 60 per cent. of the DDT immediately after spraying, even though this was much more accurately controlled than in the field. Apart from any possible inefficiency in the analytical method used, another factor would reduce the amount of DDT recovered from surface scrapings; this is the diffusion of the sorbed insecticide further into the mud. The figures in Table III of this paper could not entirely account for the rapid loss found by Pal & Sharma but may provide a partial explanation.

The postulated catalytic decomposition reaction is of a type that only proceeds under anhydrous conditions. Indeed, according to Bordas & others (1953), the soil must be dried even in the test at 130°C. Therefore, as soils in equilibrium with the atmospheric moisture are by no means anhydrous, one could not expect the reaction to proceed at room temperature. Uganda mud in equilibrium with air of 60 to 70 per cent. relative humidity contains about 3·5 per cent. of water. Other active soils all contained between 3 and 4 per cent. Previously we have shown that adsorbed DDT is decomposed in mud blocks which are kept quite dry but not in those in equilibrium with air having a greater humidity than 10 per cent. The rate of sorption is controlled by relative humidity as both Downs and his co-workers and we ourselves have shown, but this is a physical action. We cannot offer any explanation for the remarkable reactivation described by Bordas & others (1953) during a field experiment. It is difficult to imagine how sorbed DDT could return to the surface of a wall and be highly active again, particularly when a year had elapsed since the spraying. However, assuming that the high kills were due to DDT, and not to other factors, the DDT on a highly active soil had obviously not been decomposed during the year, whatever else had been happening to it.

Neither of the remaining problems, a test for activity and a method for prevention of sorption, have been satisfactorily solved. A feature of laterites is their high content of iron oxide and, as indicated in this paper, laboratory-prepared activated iron oxide is a powerful adsorbent for insecticide. Therefore it seems most likely that it is the iron oxide fraction which is the active agent in lateritic soils. As iron oxide is also an efficient catalyst for the thermal decomposition of DDT, the test of Downs & others (1951) is probably generally reliable although it should be stressed that it depends upon the coincidence that iron oxide possesses both adsorptive and catalytic properties. Thus, the Downs test will indicate that a soil probably has a high iron oxide content and therefore will probably be active but almost as much can be deduced from the visual appearance of the soils. It is by no means certain, however, that all iron oxides present in soils will have a sorptive activity even though they are active in the thermal decomposition test; a great deal will depend upon their physical condition. Also, other soil fractions might be physically but not catalytically active.

Therefore, a test which can measure the adsorptive properties more directly is to be preferred. Downs & others (1951) concluded that the inactivating properties of their soils did not depend upon adsorption because they had only low base exchange capacities. Ionic exchange capacities, however, do not indicate adsorptive properties for non-polar substances and therefore any physical test should use non-polar gases or vapours. An attempt to develop such a test has been described (p. 551) but was only partially successful. Highly active soils show high adsorptive capacities for non-polar substances such as carbon tetrachloride or benzene. Those with lower adsorption figures may or may not have some activity although, if present, this is of a lower order than that possessed by the soils with high sorptive powers. Again this test, like the thermal decomposition one, is not a great improvement on visual inspection but it can detect soils, like the Taveta sample, which are lateritic in appearance and possess a high iron content but which are relatively inefficient at sorbing insecticides. Conversely, it can detect soils such as the grey one from Taveta which are active but do not have a lateritic appearance.

Both iron-reacting substances and deliquescent salts have been sprayed on to soils at high concentrations without appreciably reducing the rate of sorption and we can only conclude with Bordas & others (1953) that limewashing of walls is the only practical preventive method that can be suggested at present. Other substances such as colloids can be used to place a barrier between the active substrate and the insecticide particles but limewash has the advantage of being porous to the spray solution and therefore wettable powders subsequently sprayed can retain their maximum efficiency. The use of insecticidal resin coatings does not prevent a loss in effectiveness, at least on active Uganda mud. The concentration of insecticide in the resin film is reduced at the time of application by penetration with the resin solvents into the mud, and is further reduced subsequently by adsorption of insecticide from the resin film into the mud.

Summary.

It is suggested that if the vapour of an insecticide is rapidly adsorbed by a substrate the rate of volatilisation of the molecules of insecticide particles lying on the substrate is greatly increased. This explains the rapid loss of effectiveness of wettable powders on some soils. After the insecticide has been sorbed it is concentrated at and near the treated surface but afterwards slowly diffuses inwards. This diffusion reduces recoveries of insecticides from surface scrapings.

DDT can be recovered quantitatively from Uganda mud blocks 12 months after sorption is complete. Therefore, on this mud at least, catalytic decomposition does not occur.

A test has been devised for measuring the sorptive capacities of soil samples for non-polar vapours. It indicates if a soil is highly active but those with lower or negligible activities do not give a good correlation.

A survey of 18 soils from different parts of the world suggests that rapid inactivation of an insecticide by sorption should be expected on any red lateritic soil. Generally, others are inert or show only low activity.

Attempts to reduce or abolish the sorptive powers of Uganda soil have not been successful and the only effective method known at present is to limewash the walls before spraying. Pretreatment with a size solution also stops sorption but, unlike limewashing, at the same time reduces the efficiency of a subsequently applied wettable powder.

Finally, work by various authors on the inactivation of insecticides on mud surfaces is reviewed.

Acknowledgements.

We are grateful to Dr. D. A. Osmond, Soil Survey of England and Wales, Harpenden; Dr. E. Bordas, Mexico; and Dr. L. Mara, W.H.O. Malaria Section, for samples of soils.

References.

BORDAS, E., DOWNS, W. G. & NAVARRO, L. (1953). Bull. World Hlth Org., **9,** pp. 39–57.

DAVIDSON, G. (1953). Bull. ent. Res., **44,** pp. 231–254.

DOWNS, W. G., BORDAS, E. & NAVARRO, L. (1951). Science, **114,** pp. 259–262.

FLECK, E. E. & HALLER, H. L. (1944). J. Amer. chem. Soc., **66,** p. 2095.

HADAWAY, A. B. & BARLOW, F. (1951). Nature, Lond., **167,** p. 854.

HADAWAY, A. B. & BARLOW, F. (1952). Bull. ent. Res., **43,** pp. 281–311.

HICKMAN, K. C. D. & TREVOY, D. J. (1952). Industr. Engng Chem., **45,** p. 1882.

KUHN, W. & MASSINI, P. (1949). Helv. chim. Act., **32,** p. 1530.

LAMBERT, B. & CLARK, A. M. (1927). Proc. roy. Soc., (A) **117,** p. 183.

MAES, H. (1952). Nature, **170,** p. 328.

PAL, Rajindar & SHARMA, M. I. D. (1952). Indian J. Malariol., **6,** pp. 251–263.

VISWANATHAN, D. K. (1952). Indian J. Malariol., **6,** pp. 265–273.

AN ECOLOGICAL STUDY OF COCCINELLIDAE (COL.) ASSOCIATED WITH *APHIS FABAE* SCOP. ON *VICIA FABA*.[1]

By C. J. Banks

Dept. of Entomology, Rothamsted Experimental Station, Harpenden.

CONTENTS.

	Page
Methods	562
Changes in Populations of Aphids on Nettles and Beans	564
Sequence of Changes in Numbers of adult Coccinellids on Nettles and Beans	565
Changes of numbers of adult Coccinellids at nettle sites	565
Changes of numbers of adult Coccinellids on the bean plots	568
Adult Coccinellids in the suction traps	571
Recaptures of marked adult Coccinellids	571
Numbers of *Coccinella 7-punctata* and *Propylea 14-punctata* at nettles	572
Effect of Changes in the Numbers of adult Coccinellids on Numbers of Eggs and Larvae on the Beans	572
Counting of eggs and larvae	572
Egg populations	572
Larval populations	575
Cannibalism	577
The fate of eggs and larvae of the second phase	579
Relations between Numbers of Coccinellids and *Aphis fabae*	581
Estimation of Mortality Rates of Coccinellids on the Bean Plots	582
Discussion	584
Summary	585
Acknowledgements	586
References	586

Some insect populations are kept in check by the action of their natural enemies which may operate as density-dependent mortality factors of the concurrent type (Solomon, 1949, p. 13). Other insect species are often very abundant in spite of natural enemies which are apparently not able to control the population in question, especially if they are able to find much of their food elsewhere. Furthermore, an insect enemy may be ineffective in reducing the numbers of a particular species if its life-cycle is not synchronised with that of the prey.

Coccinellid predators of the Black Bean Aphid, *Aphis fabae* Scop., are polyphagous and attack Aphid species on many types of plants (Smith, 1931). *A. fabae* itself is polyphagous, having a complex life-cycle involving several different host plants, and on one of its summer hosts, *Vicia faba*, enormous populations of the pest often develop. To be effective against the Aphid on any one of its host plants, the natural enemies would have to synchronise their attack with the arrival of the Aphids.

---

[1] Part of a thesis submitted for the degree of Ph.D. (University of London).

This paper describes fluctuations in numbers of Coccinellids during the spring and summer of 1952 at Rothamsted, and how they are related in time and place to populations of *A. fabae* on three experimental bean plots, and of *Microlophium evansi* (Theo.) * on stinging nettles (*Urtica dioica*), for the availability of an alternative aphid prey on nettles near the plots might influence not only the time of arrival but also the numbers of all stages of Coccinellids on the beans.

The most important species of Coccinellids, Aphid-eaters of the tribe Coccinellini, found on the nettles and bean plots were as follows:

Adalia bipunctata (L.) was the most abundant species, *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.) were common species but were not abundant, *C. undecimpunctata* L. and *A. decempunctata* (L.) were uncommon.

Methods.

The period during 1952 when field observations were made has been divided into 26 weekly intervals (Table IV), extending from 9th April until 8th October. The area studied and places mentioned in the text are shown in fig. 1.

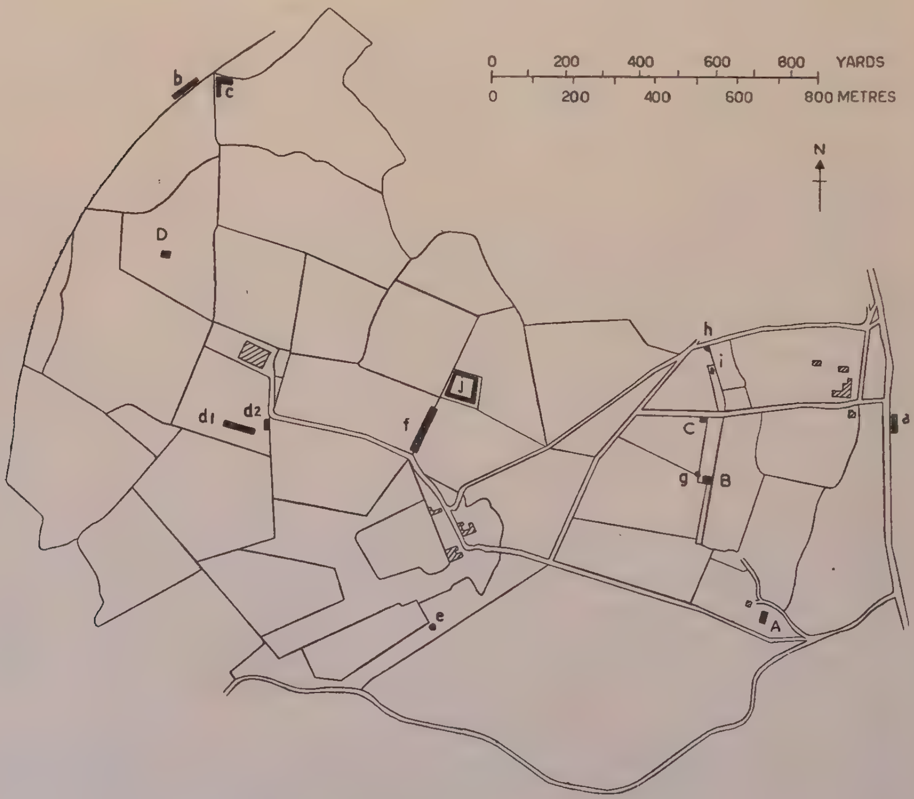


Fig. 1.—Plan of Rothamsted showing locations of bean plots A, B, C and D and places where concentrations of ladybirds were found in 1952.

---

* = *Macrosiphum urticae* (Schr.).

Nettles.

Numbers of adult Coccinellids were estimated at three selected clumps of nettles supporting large populations of ladybirds and Aphids; these were at Broadbalk (site f), Great Field II (site g), and Great Field III (site h). Each week, two observers collected all the ladybird beetles visible on the nettles during 30 minutes; after identification, the insects were liberated where found.

Bean plots.

Four experimental plots each of 12 rows, 35 ft. long and 30 in. apart, were sown with beans (*Vicia faba*) of one variety during March. The field bean used was a cross between a tick bean and broad bean.

Plot A, in Rothamsted Lodge garden, was surrounded by tall trees and buildings, and on one side was a high brick wall.

Plots B and C, about 150 yd. apart, were on Great Field II, 400–500 yd. from Plot A. They were exposed to the wind. Plot B was used only for a suction trap. Plot C was situated between two nettle sites, Great Field II and Great Field III, being only 100 yd. from each, while a large plot of beans and barley lay 300 yd. away.

Plot D, about one mile distant from the other plots, was very exposed. Surrounding crops were wheat and lucerne and some small experimental plots of potatoes and beetroot. The nearest bean field was 500 yd. away.

Towards the end of May, the numbers of stems on each plot were estimated as Plot A, 2,099 (S.E. ± 62), Plot C, 2,988 (S.E. ± 79), Plot D, 2,604 (S.E. ± 56). The plots were examined weekly for the duration of the infestations by *A. fabae* (weeks 7–15), Plot A on Tuesday, Plot C on Wednesday, and Plot D on Thursday.

The unit of sampling adopted was the bean stem, because stems rather than plants become infested with Aphids. On each plot, 13–14 per cent. of the stems were sampled by examining a fixed number of stems in each row, Plot A, 288; Plot C, 384; Plot D, 336.

Sampling was systematic in that rows were always traversed in the same order and approximately every seventh stem was examined; but sampling was started from a randomly chosen stem at the end of a row and stems were selected at ground level to avoid bias in choosing aphid-infested stems. Every leaf was scrutinised and predators counted and recorded at once but not removed from the plants.

Bean stems were classified arbitrarily according to their degree of infestation by *A. fabae*; *zero* (0), *very light* (V), *light* (L), *medium* (M) and *heavy* (H); descriptions of these classes and estimates of their numbers of Aphids for each plot have been published (Banks, 1954*c*).

Suction traps.

Two traps, with fans of 9 in. diameter, were used to supplement the data from field counts (Johnson, 1950).

Trap (a) in the centre of Plot A, ran continuously from 17th April (week 1) to 17th September (week 23); trap (b) in Plot B, ran from 4th June (week 8) to 7th October (week 26).

The traps, whose mouths were level with the tops of the beans, were emptied once each day except in the early and late weeks of the trapping periods when they were emptied every two or three days. Insects of special interest caught in the traps were Coccinellids, Syrphids, Chrysopids, Hemerobiids and Anthocorids. The daily catches were totalled each week ending on Wednesday, for comparison with the populations of Coccinellids counted on nettles and beans.

Marking of Coccinellids.

Before week 11, all captured ladybirds were marked with a spot of coloured paint on an elytron to denote the place of capture; thereafter a large proportion was labelled. The insects were always liberated within 24 hours at the places where they were found.

A variety of paints and adhesives was tested but it was difficult to find one which would adhere satisfactorily to the glabrous elytra. A cellulose paint was adopted, despite the fact that it chipped off or came off completely, sometimes leaving a dark mark on the elytron. The secretion from the thoracic glands was held partly responsible for the loss of the paint, which could not be applied if the secretion had crept on to the elytra.

Changes in Populations of Aphids on Nettles and Beans.

Large populations of Nettle Aphids (*Microlophium evansi*) were well established in week 3 on the nettle sites, Broadbalk, Great Field II and Great Field III, maximum numbers occurring approximately in weeks 7–8; by weeks 10 and 11, the numbers had fallen almost to zero.

Primary migrants of *A. fabae* arrived on all bean plots during week 6 and the infestations lasted until weeks 14 or 15.

The numbers of Aphids per stem, estimated by the method already described and published elsewhere (Banks, 1954*c*, where weeks of sampling were numbered 1–9), are plotted against weeks on arithmetic (fig. 5) and logarithmic (fig. 2) scales respectively; the former emphasises the arithmetical differences between aphid numbers of the plots while the latter shows the proportional differences and the close similarity in shape of the curves.

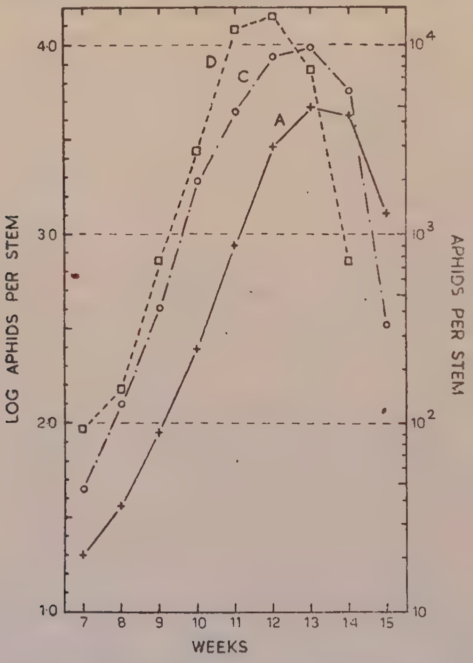


Fig. 2.—Changes in numbers of *Aphis fabae* on the bean plots A, C and D on a logarithmic scale.

The initial levels of infestation of the plots recorded in week 7 differed considerably, the percentages of infested stems being 54 per cent. on Plot D, 37 per cent. on Plot C, and 23 per cent. on Plot A, while the mean number of Aphids per stem of Plot D was more than four times that of Plot A and more than double that of Plot C.

For the first few weeks, the Aphids were confined mostly to the colonies in the crowns of small leaves (class V) but during weeks 9 and 10 the Aphids increased very rapidly and spread over the plants. The stems most heavily infested (classes M and H) formed only 1–3 per cent. of all stems at week 9 (Plots C and D) and week 10 (Plot A) but increased to 17–19 per cent. in weeks 9–10 (Plots C and D) and 10–11 (Plot A).

Aphid populations of Plots D and C multiplied enormously during weeks 8–9 and 9–10 respectively; the maximum rate of increase of population of Plot A occurred in week 10–11 and was considerably lower than that of the other plots.

Maximum densities were recorded in week 12 (Plot D) and week 13 (Plots C and A) in the ratio D:C:A::3:2:1; the areas of the curves were approximately in the same ratios.

There followed a decline in aphid numbers, very rapid on Plot D, less rapid on Plots C and A, due mainly to the departure of alatae and the loss of reproductive capacity of the apterae. The effect of parasites and predators in this decline was considered negligible in comparison with these two causes.

In week 13 at Plot D, nymphs and apterae were seen crawling off the beans on to the ground and on to nearby potatoes and beetroot and by week 14 the infestation had almost completely destroyed the plants and, as most of the leaves had fallen to the ground, no count could be made in week 15.

This investigation shows that the Aphids on nettles had become well established before *A. fabae* arrived on the beans and that bean plots of identical size within a small area, planted with the same variety of beans, may differ in several important respects as regards their populations of *A. fabae*.

The sizes of the bean-aphid populations in successive weeks and the conspicuously different maxima attained were associated with the different initial levels of infestation of the plots. The three curves in fig. 2 show that populations which were initially higher reached higher maxima, at an earlier date, and then declined correspondingly earlier, than those which were initially lower in density.

Sequence of Changes in Numbers of adult Coccinellids on Nettles and Beans.

The sequence of changes in populations of adult Coccinellids during the surveys was as follows.

Overwintered Coccinellids emerged from hibernation quarters in the spring of 1952, mated and dispersed to other habitats (Banks, 1954*a*). Many accumulated at clumps of nettles infested with *M. evansi*, and there laid large numbers of eggs which subsequently developed into a " nettle brood ". Some of the overwintered beetles then died off but most re-dispersed to other habitats, accumulating especially on bean plots after the arrival of *A. fabae*. Here they laid more eggs which developed into a " bean brood ". Before the insects of the bean brood reached the adult stage, those of the nettle brood reached maturity, mated and dispersed rapidly from nettles, many of them appearing on the bean plots, thereby augmenting the numbers of the overwintered generation already there. The bean brood reached the adult stage when the aphid infestations of the beans had finished. On the bean plots, then, three phases in changes in numbers of adult Coccinellids were apparent; (1) overwintered insects, dispersing from nettles and other places, accumulated on the beans; (2) insects of the nettle brood (progeny of overwintered Coccinellids) emigrated from nettles to beans; (3) a bean brood (also progeny of the overwintered Coccinellids) appeared at the end of the aphid infestations.

Changes of numbers of adult Coccinellids at nettle sites.

At the end of April and early in May, a search was made for Coccinellids newly-emerged from hibernation. Many clumps of stinging nettles (*Urtica dioica*) were searched and although individual insects were occasionally found,

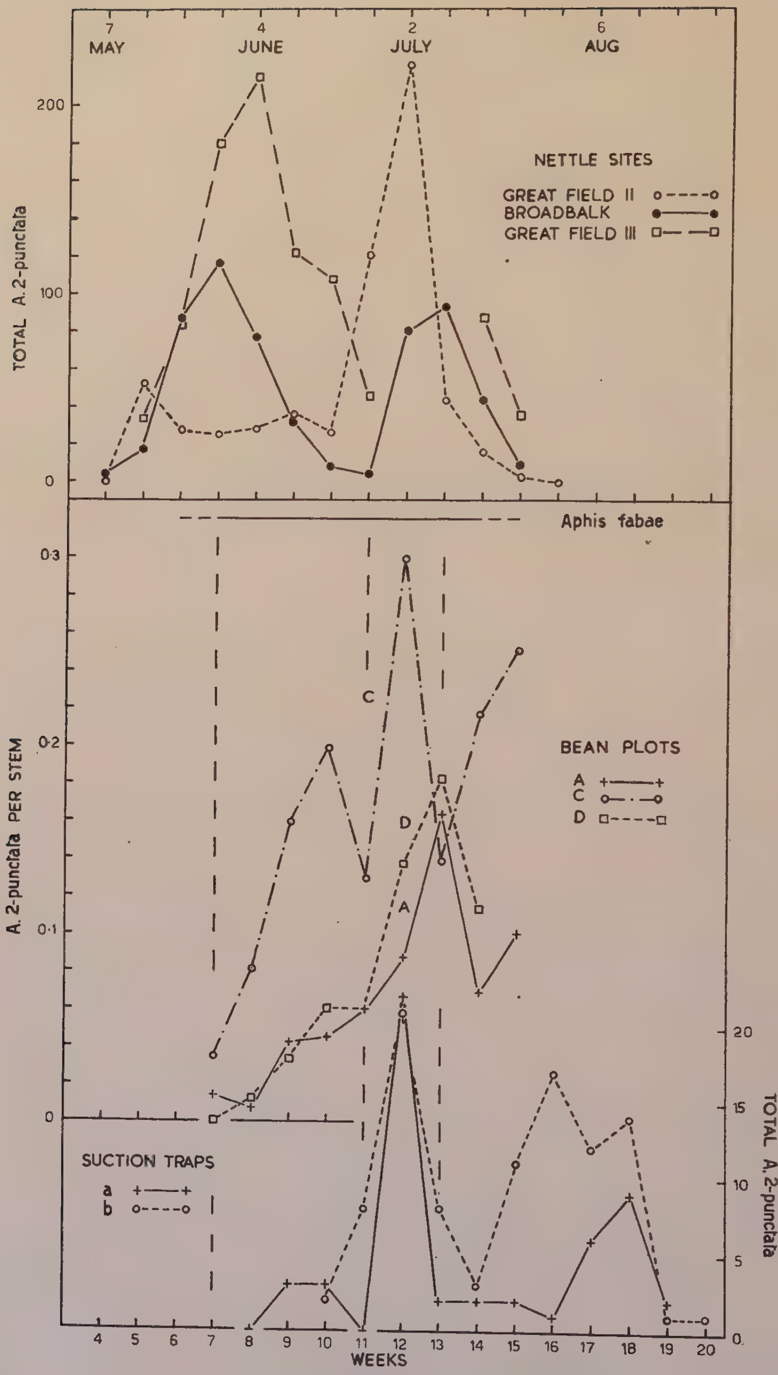


Fig. 3.—Changes in numbers of adult *Adalia 2-punctata* at nettle sites, bean plots and in suction traps, 1952.

concentrations occurred only at the places listed in Table I. Coccinellids were most abundant at the nettle sites at Broadbalk, Great Field II and Great Field III which were heavily infested with *M. evansi*, while at all other nettles Aphids were scarce or absent. There were probably many other places where

TABLE I.

Concentrations of overwintered ladybirds at Rothamsted; maximum numbers counted during April and May 1952.

	Site	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*C. 11-punctata*
Harpenden Common (grass)	a	111	0	0	12
West Barnfield (grass) ..	b	40	0	0	0
Sawyers (nettles)	c	7	0	0	0
Little Knott (beans) ..	d1	11	0	0	0
Little Knott (nettles) ..	d2	6	0	0	0
Highfield (nettles) ..	e	7	0	3	0
Broadbalk (nettles) ..	f	108	137	47	0
Great Field II (nettles) ..	g	27	60	9	0
Great Field III (nettles) ..	h	37	218	13	0
Bee enclosure (nettles) ..	i	*ca.*10	0	0	0
Kitchen Garden (nettles) ..	j	0	*ca.* 6	0	0

Aphids and Coccinellids occurred but those examined had the largest numbers of ladybirds and probably formed a large part of the total ladybird population of the neighbourhood.

The most abundant species of Coccinellid at the nettle sites was *Adalia 2-punctata* whose numerical changes are shown in fig. 3. For comparison with the weekly counts on bean plots, the records at nettle sites (Table II) have been adjusted by interpolation to give an estimate of numbers of ladybirds on Wednesday of each week (fig. 3). The records for *C. 7-punctata* and *P. 14-punctata*, which were less abundant, are discussed below (p. 572).

The numbers of overwintered *A. 2-punctata* rose to a maximum in weeks 7 and 8 and then declined as the insects re-dispersed, although some died at this time. Numbers of all species of Coccinellids on nettles were lowest during weeks 9–11 but populations of larvae and pupae had already risen during weeks 5–11, developed from eggs laid earlier by the overwintered generation.

In weeks 11 and 12 there were rapid increases to second maxima at the nettle sites as the new brood emerged from the pupae. This change was especially noticeable in *A. 2-punctata* but similar changes occurred in *C. 7-punctata* and *P. 14-punctata* whose numbers were much lower. The new maxima were followed by rapid declines as the newly-emerged adults dispersed; Aphid populations of the nettles at this time had almost completely disappeared and the ladybirds were without food.

Each of the three common species of Coccinellids, therefore, developed one brood on the nettles from the overwintered insects.

TABLE II.

Records of adult Coccinellids counted at three nettle sites, 1952.

	Broadbalk (site f)				Great Field II (site g)				Great Field III (site h)			
	C. 7-punctata	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*
May 5	108	2	0	0								
7					31	1	0	0				
9									37	4	6	1
12	78	8	1	0								
13	53	8	6	1	45	60	3	1				
16					14	33	1	0	14	45	10	0
17	74	0	0	0								
20	51	67	21	0								
21					9	27	7	0				
23	50	131	47	0								
24									7	106	13	1
26	38	137	30	0								
27					1	25	0	2				
29	16	106	13	0								
30									3	218	6	4
June 1	22	87	4	0								
3					0	26	0	1				
6	4	71	4	1					3	212	0	4
9					4	37	1	0				
13	3	17	4	0					6	101	2	0
16					5	29	0	0				
20	3	5	0	1					2	109	0	9
22					5	19	1	4				
27	21	4	0	0					31	18	0	0
30					25	300	4	9				
July 5	19	126	1	0								
6					6	58	4	1				
11	5	76	1	1								
13					0	23	0	3	17	109	0	3
18	1	29	0	1								
20					0	6	0	0	3	57	1	3
25	0	0	0	0								
26					0	0	0	0				
27									2	6	0	0

Changes of numbers of adult Coccinellids on the bean plots.

A. fabae arrived on the beans during week 6; maximum densities of Aphids were reached in weeks 12 or 13 and the infestations lasted until weeks 14 or 15.

Some Coccinellids were present on the bean plots before the arrival of the Aphids and, on Plot D in week 6, batches of coccinellid eggs and even well-developed larvae of *C. 7-punctata* were found, indicating that oviposition must have occurred at this plot several weeks before but had escaped notice. These larvae had probably fed as cannibals.

The total numbers of all stages of Coccinellids counted on the bean plots are given in Table III. The most abundant species was *A. 2-punctata* which formed 67–76 per cent. of all Coccinellids found on the plots and the following description of events refers to this species (fig. 3).

Plot C was noted for its comparatively high density of ladybirds at all times; populations of Plots A and D were lower. On each plot, three phases in the changes in populations of *A. 2-punctata* were distinguished.

Phase 1 (weeks 7–11) was a period when numbers were comparatively low on all plots, but the maximum population of adult Coccinellids at Plot C was

TABLE III.

Total numbers of Coccinellids of all species counted on the bean plots A, C and D.

Week	Adults					Eggs	Larvae			Pupae
	A. 2-punctata	*P. 14-punctata*	*C. 7-punctata*	*Others*	*Total*		just hatched	older larvae	all larvae	
Plot A										
7 ..	4	5	0	0	9	154	0	0	0	0
8 ..	2	10	0	0	12	327	13	0	13	0
9 ..	12	4	0	0	16	232	18	8	26	0
10 ..	13	3	0	0	16	571	34	17	51	0
11 ..	17	0	0	0	17	270	52	40	92	0
12 ..	25	4	3	0	32	1,293	14	148	162	26
13 ..	47	10	3	5	65	979	45	231	276	70
14 ..	20	9	0	2	31	538	52	229	281	31
15 ..	29	4	10	1	44	21	8	138	146	32
Totals ..	169	49	16	8	242	4,385	236	811	1,047	159
Plot C										
7 ..	13	13	1	0	27	456	0	0	0	0
8 ..	31	17	3	0	51	537	25	4	29	0
9 ..	61	12	3	0	76	1,392	4	24	28	0
10 ..	76	6	11	0	93	2,444	139	122	261	0
11 ..	49	2	4	4	59	1,883	108	222	330	4
12 ..	115	23	34	1	173	3,527	28	659	687	85
13 ..	53	31	15	3	102	1,193	15	430	445	328
14 ..	83	28	6	2	119	215	12	390	402	130
15 ..	96	2	32	2	132	6	0	103	103	63
Totals ..	577	134	109	12	832	11,653	331	1,954	2,285	610
Plot D										
7 ..	0	4	2	0	6	249	13	0	13	0
8 ..	4	1	0	0	5	180	11	4	15	0
9 ..	11	8	0	0	19	324	47	4	51	0
10 ..	20	3	0	1	24	616	17	22	39	0
11 ..	20	3	3	1	27	527	31	68	99	1
12 ..	46	16	7	2	71	2,922	34	236	270	58
13 ..	61	10	12	5	88	1,794	16	233	249	112
14 ..	38	27	1	2	68	323	30	318	348	105
Totals ..	200	72	25	11	308	6,935	199	885	1,084	276

considerably higher than those of Plots A and D. The insects of this phase were overwintered Coccinellids which arrived on the beans before and during the early stages of the aphid infestation; as the ladybird numbers on nettles declined during these weeks, those of bean plots increased.

Phase 2 (weeks 12–13 Plot C; 12–14 Plots A and D) was characterised by a sudden rise in numbers in week 12, the cause of which was an immigration to the bean plots of ladybirds, mostly *A. 2-punctata*, developed from eggs laid earlier on the nettles by the overwintered beetles (nettle brood). Aphid populations on beans had now reached their highest densities.

On Plot C, a maximum density of ladybirds was quickly attained, for this plot was situated close to the two nettle sites Great Field II and Great Field III, both of which had high populations of ladybirds. On the other hand, Plots A and D reached their maxima a week later (week 13); they were remote from nettle sites and Plot A was sheltered by tall trees and buildings. The maximum of Plot C was again high in comparison with the maxima of Plots A and D which were almost identical in this phase. The end of the phase was characterised by a sharp fall in numbers as the insects died off and dispersed.

Phase 3 (weeks 14–15) was a second rise in numbers after the decline at the end of the second phase, and resulted from the emergence of Coccinellids

TABLE IV.

Weekly totals of adult Coccinellids captured in suction traps a and b.

Week ending	Week No.	Trap a						Trap b						
		A. 2-punctata	*P. 14-punctata*	*A. 10-punctata*	♂♂	♀♀	Total	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*	♂♂	♀♀	Total
April 16 ..	1	0	0	0	0	0	0							
23 ..	2	0	0	0	0	0	0							
30 ..	3	0	0	0	0	0	0							
May 7 ..	4	0	0	0	0	0	0							
14 ..	5	0	0	0	0	0	0							
21 ..	6	0	2	0	1	1	2							
28 ..	7	0	0	0	0	0	0							
June 4 ..	8	0	0	0	0	0	0	0	0	0	0	0	0	0
11 ..	9	3	0	0	2	1	3	0	0	0	0	0	0	0
18 ..	10	3	3	0	2	4	6	0	2	0	0	2	0	2
25 ..	11	0	0	0	0	0	0	0	8	0	0	8	0	8
July 2 ..	12	22	1	0	18	5	23	0	21	0	1	17	5	22
9 ..	13	2	0	0	1	1	2	2	8	1	1	9	3	12
16 ..	14	2	1	1	4	0	4	0	3	1	1	4	1	5
23 ..	15	2	1	0	2	1	3	1	11	3	0	7	8	15
30 ..	16	1	1	0	2	0	2	0	17	0	1	7	11	18
Aug. 6 ..	17	6	0	0	4	2	6	0	12	1	0	4	9	13
13 ..	18	9	0	0	4	5	9	2	14	1	0	3	14	17
20 ..	19	2	1	0	1	2	3	0	1	0	0	0	1	1
27 ..	20	0	0	0	0	0	0	0	1	0	0	0	1	1
Sept. 3 ..	21	0	0	0	0	0	0	0	0	0	0	0	0	0
10 ..	22	0	0	0	0	0	0	0	0	0	0	0	0	0
17 ..	23	0	0	0	0	0	0	0	0	0	0	0	0	0
24 ..	24							0	0	0	0	0	0	0
Oct. 1 ..	25							0	0	0	0	0	0	0
8 ..	26							0	1	0	0	0	1	1
Total		52	10	1	41	22	63	5	99	7	4	61	54	115

developed from eggs laid on the beans also by the overwintered beetles (bean brood). Aphid populations of the plots had fallen rapidly. No results could be obtained for Plot D in this phase as counts had to be discontinued after week 14, the infestation being finished and the plants nearly completely defoliated. Many Coccinellids and other predators of the Aphids were found in the accumulated litter on the ground at Plot D at this time (see p. 579).

The three phases were shown also by the population changes of *C. 7-punctata*, especially on Plot C, the numbers of this species being much smaller than, and the phases not so distinct as, those of *A. 2-punctata*. The numbers for *P. 14-punctata* were too small to allow separate analysis.

Adult Coccinellids in the suction traps.

Further evidence on the changes in populations of adult Coccinellids on the beans and nettles are given by the results from the two suction traps (Table IV). The records for *A. 2-punctata*, shown in fig. 3, reflect the three phases already observed.

During the period weeks 6–20, the numbers of Coccinellids of all species captured in Trap a (Plot A) was 63 (maximum, 23 in one week) while in Trap b (Plot B), 114 Coccinellids (maximum, 22 in one week) were obtained.

Recaptures of marked adult Coccinellids.

Movements of ladybirds between sites selected for study were also investigated by marking the insects with coloured paints before liberation at the sites where they had been captured.

TABLE V.

Records of Coccinellids marked and liberated at sites where first found and recaptured elsewhere.

Date of recapture	Week	Species	Liberated at	Recaptured at	Remarks
16 May	6	*C. 7-punctata*	Site e	Site h	Liberated site e on 12 May. Seen again site h on 24 May
16 May	6	*P. 14-punctata*	Site g	Plot B	
23 May	7	*C. 7-punctata*	Site d, f or g	Plot D	Paint missing
24 May	7	*A. 2-punctata*	Site g	Site h	
9 June	9	*A. 2-punctata*	Site g or Plot B	Plot A	Recovered on mustard near Plot A; paint missing
11 June	9	*A. 2-punctata* *P. 14-punctata*	Site g	Plot C	
18 June	10	*C. 7-punctata*	Site g, Plot B or C	Plot C	Two specimens, probably from site g; paint missing from both specimens
2 July	12	*A. 2-punctata*	Site h	Plot C	

Marked Coccinellids were often found again where they had been liberated; only a few were recovered, however, at other sites (Table V); this is attributed primarily to the fact that the area over which the insects could disperse was very large in comparison with the part studied. Furthermore, the unsatisfactory marking technique was partly responsible for the paucity of the results.

Numbers of Coccinella 7-punctata *and* Propylea 14-punctata *at nettles.*

Changes in numbers of *C. 7-punctata* and *P. 14-punctata* at the three nettle sites were similar to those of *A. 2-punctata* except that in weeks 4 and 5 the numbers of *C. 7-punctata*, already at a high value, had started to decline, due partly to re-dispersal and partly to mortality (several specimens parasitised with the Braconid, *Perilitus coccinellae* (Schr.) were found in early spring). *C. 7-punctata* apparently emerged from hibernation earlier than the other two and appeared at the nettles at least four weeks before them. This is supported by observations at Great Field II nettles where, in week 5, many *A. 2-punctata* were found under dried leaves close to the nettles and in a state of lethargy, not then ready to disperse.

But the second peaks (nettle brood) of *C. 7-punctata* and *A. 2-punctata* coincided; which is explained by the difference in average length of the life-cycles of the species: *C. 7-punctata* 44 days, *A. 2-punctata* 37 days, and *P. 14-punctata* 27 days. The second peak of *P. 14-punctata* was too small to allow any conclusions to be drawn.

Effects of Changes in the Numbers of adult Coccinellids on Numbers of Eggs and Larvae on the Beans.

Numbers of eggs and larvae of Coccinellids on the bean plots corresponded to variations of the adult insects both in phase and in numbers, with the important exception that there was no third phase of the immature stages to correspond to the third phase of adults. In addition, two effects of special significance will be described, namely, cannibalism and the probable death through starvation of many larvae of the second phase.

Counting of eggs and larvae.

The eggs of *A. 2-punctata*, orange in colour, are laid in batches containing an average of 12·5 eggs and usually occur on the undersides of leaves on the middle of the plants, although occasionally near the top. Eggs of *C. 11-punctata* could not be distinguished from those of *A. 2-punctata*. Eggs of *P. 14-punctata* are yellow and the batches have an average of 6·5 eggs, occurring underneath the bottom leaves, frequently on the pair closest to the ground. Eggs of *C. 7-punctata* are orange, larger than those of *A. 2-punctata*, and the batches have an average of 25 eggs although as many as 65 in a batch have been counted; they occur usually underneath the leaves but occasionally on the upper surfaces and sometimes at the tops of the plants.

Despite these differences, some eggs could not be assigned to a species. Eggs of *A. 2-punctata* appeared to form 70–78 per cent. of all eggs counted on the three plots. Eggs of all species have been treated together, especially for comparison with numbers of the larvae.

In the field, species of larvae could not be distinguished in the early instars which often cannot be seen after the insects have dispersed from the egg shells; third and fourth (final) instars are usually readily seen and identified.

Larvae of all species, therefore, have been treated together and were classified as " just hatched " (1st instar larvae still grouped on the empty egg shells before dispersal, a stage lasting up to 24 hours) and as " older larvae " (mostly 3rd and 4th instars with a few earlier-stage larvae).

Egg populations.

Considerable fluctuations in numbers of eggs occurred on all plots (Table III; fig. 4). While two phases may be discerned, corresponding to the first two phases in the populations of adults, there was no third phase to correspond to the third phase of adults.

Phase 1 (weeks 7–11) was characterised by a comparatively low egg density on all plots, synchronous with that of adults. Plot C reached a much higher maximum egg density during this phase than did Plots A and D.

Phase 2 (weeks 11–14 or 15) attained a much higher egg density than the first and corresponded to the second phase of adults; the egg density of Plot D was higher than that of Plot A and almost equal to that of Plot C.

At Plots A and D, the second maximum of eggs was reached in week 12, one

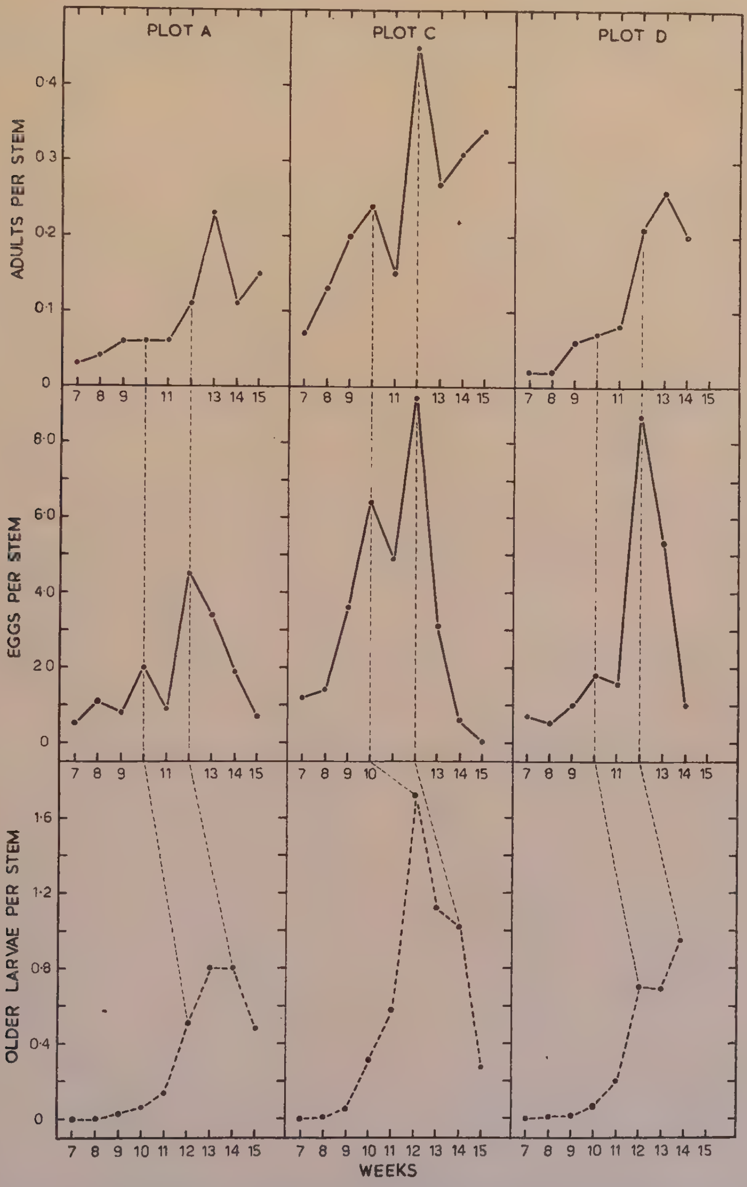


Fig. 4.—Comparison of the numerical changes of adults, eggs and older larvae of all species of Coccinellids for the bean plots A, C and D during the infestations by *Aphis fabae*.

week before the maximum density of adults. These two plots, being remote from nettles, received the nettle brood immigrants over a period of two weeks; the first immigrants laid large numbers of eggs in week 12 but as adults continued to arrive, the numbers of eggs in week 13 were maintained at a comparatively high level. On the other hand, during week 12, Plot C, which was close to nettle sites g and h, was invaded by many ladybirds which at once laid large numbers of eggs; as few immigrants arrived during week 13, the numbers of eggs at this plot, therefore, fell very rapidly.

The absence of a third phase of eggs indicates that the adult Coccinellids, which developed from eggs laid on the beans during phase 1 (bean brood), did not lay eggs; indeed, no third phase adults were observed to mate (Table VI).

TABLE VI.

Records of pairs of Coccinellids seen *in copula* on the bean plots A, C and D.

	Weeks								
	7	8	9	10	11	12	13	14	15
Plot A									
A. 2-*punctata*	0	0	1	2	2	1	2	0	0
P. 14-*punctata*	1	1	0	0	0	0	0	0	0
C. 7-*punctata*	0	0	0	0	0	0	0	0	0
Total ..	1	1	1	2	2	1	2	0	0
Plot C									
A. 2-*punctata*	0	1	11	6	7	10	1	0	0
P. 14-*punctata*	0	1	1	1	0	0	0	0	0
C. 7-*punctata*	0	0	0	0	0	1	0	0	0
Total ..	0	2	12	7	7	11	1	0	0
Plot D									
A. 2-*punctata*	0	0	3	3	2	0	2	0	
P. 14-*punctata*	0	0	3	0	0	0	0	0	
C. 7-*punctata*	0	0	0	0	0	0	0	0	
Total ..	0	0	6	3	2	0	2	0	
Grand Total	1	3	19	12	11	12	5	0	0

The first two phases of adult Coccinellids, then, were reflected by corresponding phases in egg numbers. Plot C had a large number of eggs during both phases while Plot A had a comparatively low density of eggs at all times.

Larval populations.

Counts of larvae (Table III; figs. 4, 5) reveal two facts, (1) the absence of distinct phases to correspond with those of egg populations, (2) that the densities of larvae of the three plots differed from each other. These problems are considered below.

(1) The absence of distinct phases in curves for larvae, which were such a noticeable feature of adult and egg populations, is noteworthy, but the existence

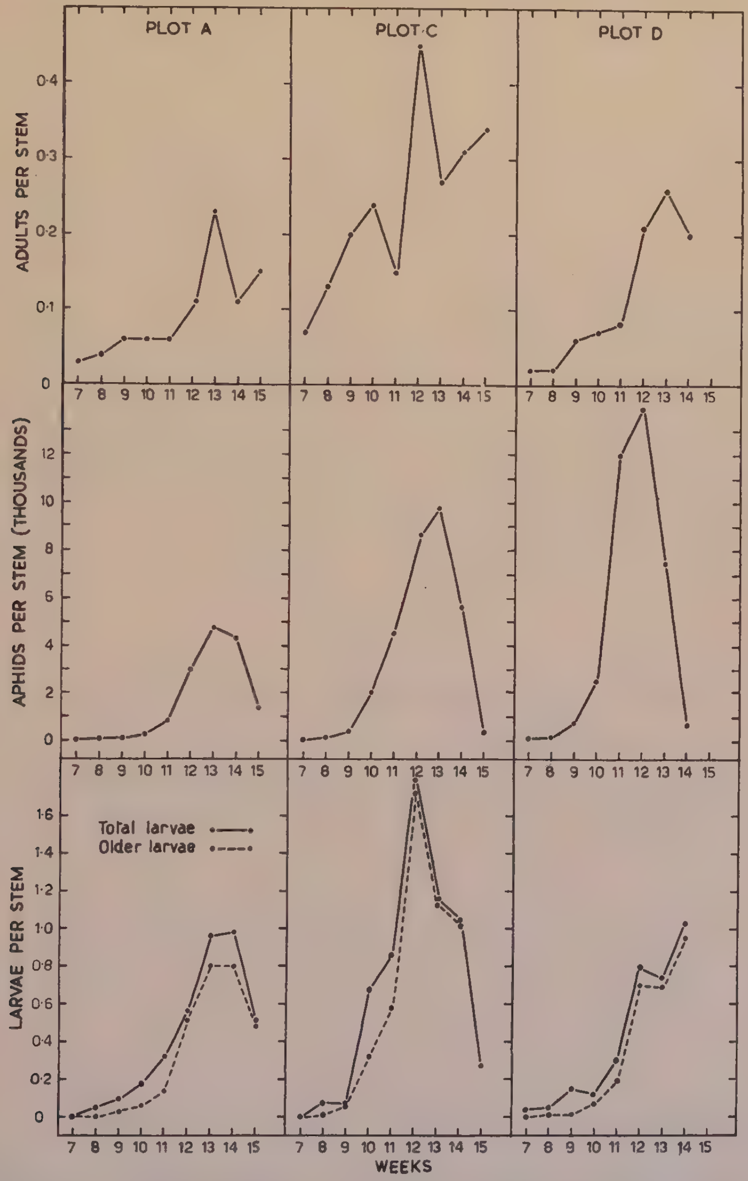


Fig. 5.—Comparison of the numerical changes of adults and larvae of all species of Coccinellids with the changes in numbers of *Aphis fabae* on the bean plots A, C and D.

of these phases may be discerned on Plots C and D. As the egg stage lasts for an average of seven days and the young larvae (1st and 2nd instars) would not be counted for another seven days ("missing stage"), the total lag between counting the eggs and the resulting older larvae would be approximately 14 days. It should, therefore, be possible to associate the eggs counted in one week with the older larvae counted two weeks later. This may be done satisfactorily for Plots C and D, when the peaks of egg numbers in phases 1 and 2 may be seen reflected in the populations of older larvae (fig. 4).

The maximum of eggs in week 10 (phase 1) resulted in a maximum of older larvae in week 12, while the second maximum of eggs (week 12) produced older larvae in week 14, giving a rise in numbers of larvae on Plot D as expected; but on Plot C there was no rise in numbers owing to the high rate of pupation in week 13; instead, there was a check in the decline of older larvae.

The older larvae curve for both Plots C and D is smooth and regular from weeks 7–12; after that it would have dropped rapidly as the larvae pupated. Instead, the fall of the population in week 14 was checked (Plot C) or the density actually rose (Plot D), due to the heavy rate of oviposition in week 12. The drop in numbers on both plots during week 13 was, of course, partly caused by the decline in numbers of eggs in week 11.

For Plot A, however, the phases are obscured. Instead of an expected drop in numbers of older larvae in week 14, numbers remained the same as in the week before, because the eggs laid in week 12 counter-balanced the number of larvae pupating in week 14. The usual drop due to pupation was not recorded, therefore, until week 15; maxima of pupae occurred in week 13 on all plots (Table III).

(2) Densities of total larvae of Plot C were always much higher than those of Plots A and D; this was not unexpected in view of the large populations of adults and eggs recorded on Plot C. There is, however, a positive correlation in both phases 1 and 2 between the maximum densities of adults (of all species), eggs and larvae of each plot (Table VII).

TABLE VII.

Correlations between maximum densities of Coccinellid adults (all species), eggs and larvae of the bean plots A, C and D.

	Plot	Adults per stem	Eggs per stem	Total larvae per stem
Phase 1	C	0·24	6·37	1·79
	A	0·06*	1·98	0·96
	D	0·08*	1·83	0·80
Phase 2	C	0·45	9·19	1·16
	D	0·26	8·70	1·03
	A	0·23	4·49	0·98

* The population densities of adult insects on Plots A and D were very low in phase 1 and these differences are probably not significant.

It may be concluded therefore, that the populations of eggs and larvae were correlated with the populations of adult Coccinellids on each plot, both as regards the phases (1 and 2) and in population densities.

Cannibalism.

An irregularity in the curve for total larvae for Plot C occurred in weeks 10 and 11 (fig. 5). Many just-hatched larvae were counted in those weeks, because of the high rates of oviposition in weeks 9 and 10, respectively. In week 10 there was a greater increase in the density of eggs than in week 9 and it would have been expected, therefore, that the density of just-hatched larvae in week 11 would have been similar to, or even greater than, that in week 10. This was not the case, for there was a marked falling-off in density of just-hatched larvae in week 11. An approximate estimate of this "loss" may be made.

The duration of the egg stage is about seven days and the just-hatched stage lasts from a few hours to one day. An estimate of the numbers of eggs laid on any one day may be obtained by dividing the total number of eggs counted by the duration of the stage (p. 583), thus:

	Eggs counted	Estimate of egg population		Just-hatched larvae counted
Week 9	1,392	199	Week 10	139
Week 10	2,444	349	Week 11	108

If 199 eggs in week 9 produced 139 just-hatched larvae in week 10, then 349 eggs in week 10 might have been expected to produce 244 just-hatched larvae in week 11; as only 108 were counted, there was, therefore, an approximate loss of 136 just-hatched larvae or about 56 per cent. of the expected value.

This loss was attributed to the destruction of the eggs by the larvae, especially by those of the early stages.

On all three plots, larvae of both *A. 2-punctata* and *P. 14-punctata* were seen attacking their own and each other's eggs at various times: this intra-specific and inter-specific predation will be referred to, for convenience sake, as cannibalism.

All instances of larvae and adults seen attacking eggs or other stages are recorded in Table VIII. Predation of eggs by larvae during phase 1 was

TABLE VIII.

Records of cannibalism (destruction of eggs by larvae) on the bean plots A, C and D, with densities of Aphids and coccinellid eggs.

	Week	Frequency of cannibalism	No. of cannibal larvae	Cannibal larvae as proportion of older larvae (%)	Aphid numbers (Aphids/stem)	Coccinellid egg numbers (eggs/stem)
Plot C	7	0	0	0	45	1·19
	8	1	1	25·0	125	1·40
	9	3	6	25·0	403	3·63
	10	16	22	18·8	1,917	6.37
	11	8	12	5·4	4,458	4·90
	12	2	2	0·3	8,628	9·19
	13	1	2	0·5	9,639	3·11
	14	0	0	—	5,738	0·56
	15	0	0	—	331	0·02
Plot A	9	1	1	12·5	90	0·81
	10	2	5	29·4	248	1·98
	13	1	1	0	4,676	3·40
Plot D	9	1	1	25·0	720	0·96
	12	1	3	1·2	13,958	8·70
	13	1	1	0	7,459	5·34

TABLE IX.

Records for Plot C of cannibalism (egg destruction by larvae) on the 30 bean stems on which it was observed.

Week	No. of cannibal larvae	No. of older larvae not cannibals	Proportion of cannibal larvae of all older larvae (%)	No. of stems	Mean Aphids on these stems	Mean coccinellid eggs on these stems	No. of cannibal larvae, no. of stems concerned and class of stem				
							Class of stem				
							O	V	L	M	H
7	0	—	—	—	—	—					
8	1	0	100	1	97	12		1(1)			
9	6	1	86	3	1,212	12		1(1)	5(2)		
10	22	11	67	15	2,212	22	2(2)	11(8)	3(1)	6(4)	
11	12	9	57	8	4,019	15		4(3)	2(2)	5(2)	1(1)
12	2	2	50	2	10,335	18				1(1)	1(1)
13	2	4	33	1	13,010	12					2(1)
14	0	—	—	—	—	—					
15	0	—	—	—	—	—					

frequently observed on Plot C, rarely on Plots A and D. The total occasions seen, during a period of about 6 hours in one day per week, of larvae eating eggs were: Plot A, 4; Plot C, 32; Plot D, 3. Plot C was conspicuous, therefore, also in this respect.

Cannibalism on Plot C resulted from the high population of coccinellid eggs during phase 1 before Aphids had become abundant. In week 9 only 3 per cent. of the stems examined had large, well-developed Aphid populations (classes M and H); in week 10, 17 per cent. of the stems were classified together as M and H, for aphid colonies had increased very rapidly and the Aphids had spread over the plants.

Coccinellid eggs were also increasing in number and in week 10 reached a maximum density of approximately 6·4 eggs per stem (Table VIII). It was from the eggs counted in week 10 that the loss of just-hatched larvae in week 11 was observed. In week 10, nearly 70 per cent. of all larvae seen on the 15 stems concerned were feeding on eggs, yet the average number of Aphids on those stems was 2,212 and the mean number of eggs was only 22 per stem (Table IX).

Although cannibalism was associated with a scarcity of Aphids on the one hand and an abundance of eggs on the other during the first phase, the most important factor was the high density of eggs, associated with the relative locations of eggs and Aphids on the bean stems; Aphids were mostly on the tops of the stems, while coccinellid egg batches were situated on the undersurfaces of the leaves low on the plants; furthermore, egg batches were often laid on uninfested stems. Larvae dispersing from the egg shells after hatching would probably encounter egg batches more readily than they would aphid colonies.

That cannibalism was not just a question of the relative abundance of Aphids or eggs is further supported by the evidence of Table IX. Cannibalism not only occurred on stems where Aphids were scarce (classes O, V and L) but also where they were abundant (classes M and H), although less frequently. For example, on Plot C in week 10, 6 cannibal larvae were recorded on 4 stems of class M, each of which had, on the average, 7,660 Aphids and only 25 coccinellid eggs.

The fate of eggs and larvae of the second phase.

On Plot D, the Aphids reached their maximum numbers in week 12, with an average of approximately 14,000 Aphids per stem. During week 13, many apterae and nymphs had crawled off the plants on to the ground and on to nearby plants, and by week 14 the aphid population of the plot had declined almost to zero. Aphids had been so numerous that the plants were killed and defoliated, many predators falling to the ground.

In order to determine the fate of the large numbers of larvae of week 14, resulting from the high rate of oviposition in week 12, an examined was made of the accumulated litter on the ground at Plot D during week 14, immediately after the last count on the bean stems.

All the dried leaves and some loose soil were collected from a quadrat 13 in. square, four times per row, the 48 samples being equivalent to $\frac{1}{8}$th of the area occupied by the bean stems. The samples were enclosed in paper bags and sorted in the laboratory.

In the samples from Plot D, there were 66 adult Coccinellids, 99 larvae and 51 pupae (Table X). The last would probably have survived in the field and indeed did in the laboratory; whether the larvae would also have survived is very doubtful. Some might have been able to do so by preying on other insects or on each other and some would have been ready to pupate; the majority would probably have died.

The 99 larvae were equivalent to a density of 0·30 larvae per stem; the actual density on the stems in week 14 was 1·04; thus, approximately 22 per cent. of the total larvae of week 14 was in the litter on the ground. Similarly, 50 per cent. of the adult Coccinellids and 33 per cent. of the pupae were also in the litter.

Similar samples were taken at Plots C and A in weeks 15 and 16, respectively, but much smaller numbers of Coccinellids were found in the litter. Defoliation of the plants at these plots was slight in comparison with that at Plot D.

TABLE X.

Coccinellids recorded in 48 samples of the ground litter at Plots D, C and A.

	Adults				Eggs	Larvae	Pupae
	A. 2-punctata	*P. 14-punctata*	*C. 7-punctata*	*C. 11-punctata*			
Plot D (week 14)							
Total in litter	13	13	0	40	20	99	51
Equivalent density/stem			0·20			0·30	0·15
Actual density/stem			0·20			1·04	0·31
Per cent. in litter			50·0			22·3	32·8
Plot C (week 15)							
Total in litter	44	3	6	0	0	35	44
Equivalent density/stem			0·12			0·09	0·12
Actual density/stem			0·34			0·27	0·16
Per cent. in litter			26·5			25·6	41·4
Plot A (week 16)							
Total in litter	17	2	1	0	0	1	15
Equivalent density/stem			0·07			0·01	0·05
Actual density/stem			0·15			0·51	0·11
Per cent, in litter			31·4			0·8	32·3

There was no means of telling whether the adult Coccinellids would have overwintered on the soil as, following normal practice, the plots were cleared of the beans a few weeks later. Plot C was cleared during August and no adult Coccinellids were found on the ground during the work.

The large number of eggs laid on Plot D during week 12, therefore, produced a comparatively large number of larvae in week 14, many of which probably died of starvation. The nettle brood had arrived on the beans and laid these eggs when the Aphids there had already reached their maximum numbers. These eggs were probably wasted. On Plots A and C, the decline of aphid numbers was not so rapid and larvae on the bean plots from the nettle brood had a food supply available for a longer period.

Relations between Numbers of Coccinellids and *Aphis fabac.*

The rates of growth, times of reaching maximum densities and the rates of decline of Aphid populations of the three plots differed and adult coccinellid populations were not closely synchronised with them (fig. 5). Furthermore, the numbers of adult Coccinellids entering the plots showed no obvious dependence on the numbers of Aphids there; for, Plot D had a high aphid population and a low population of ladybirds, Plot C, with an intermediate aphid population, had the highest coccinellid numbers of all plots, while Plot A had comparatively few Aphids and low numbers of ladybirds.

Populations of coccinellid larvae depended on the numbers of eggs laid, which in turn were dependent on the numbers of adults coming on to the plots and apparently not on the relative amounts of aphid food available. Where Aphids were more abundant, however, fewer larvae might die as the result of a difficulty in finding prey (Nicholson, 1933, p. 167) and if the quantity of food available was always a limiting factor, the survival rates of the larvae would be correlated with the density of the Aphids. We may not, however, compare the final survival rates of Coccinellids (Table XI) with the aphid densities of the plots, for the causes of mortality were multiple (see below) (Thompson, 1939, p. 361; Ullyett, 1953, p. 78).

The most critical time in the life of the larvae is probably after eclosion when the insects have dispersed from the egg shells; prey density is probably then a limiting factor in survival. When a larva has reached a food supply sufficient for its further development, its chances of survival are probably much enhanced and the importance of food supply as a limiting factor in survival is decreased. Prey density would, then, probably be most important between the just-hatched and older larvae stages; but the mortality rates between these stages were not correlated with the aphid densities of the three plots.

While the presence of *Aphis fabae* on the beans was the cause of the accumulation of the ladybirds on the plots, the levels of populations of the predators

TABLE XI.

Estimation of populations and mortality of immature stages of Coccinellids on the bean plots A, C and D.

Corrections for fauna in litter.

		Plot		
		A	C	D
1. Proportion in litter (%) (Table X)	larvae	0·8	25·6	22·3
	pupae	32·3	41·4	32·8
2. No. in litter (calculated)	larvae	1	35	99
	pupae	15	44	51
3. Total counted week 7–15 (Table III)	eggs	4,385	11,653	6,935
	larvae	1,047	2,285	1,084
	pupae	159	610	276
4. Corrected totals (2+3)	eggs	4,385	11,653	6,935
	larvae	1,048	2,320	1,184
	pupae	174	655	327

Corrections for duration of stage.

	Duration of stage (days)	Estimated populations Plot		
		A	C	D
Eggs	7	4,385	11,653	6,935
Just-hatched larvae ..	0·5	3,304	4,634	2,786
Older larvae	14	406	995	493
Pupae	9	135	509	254

Mortality rates (per cent.).

	Plot		
	A	C	D
Eggs—just-hatched larvae ..	24	60	60
Just-hatched larvae—older larvae	88	79	82
Older larvae—pupae	67	49	49
Eggs—pupae	96·9	95·7	96·3
Survivors to pupal stage ..	3·1	4·3	3·7

Mortality (per 100 eggs).

	Plot					
	A		C		D	
	died	survived	died	survived	died	survived
Eggs	24	76	60	40	60	40
Just-hatched larvae ..	67	9	32	8	33	7
Older larvae	6	3 pupae	4	4 pupae	3	4 pupae

were not determined by the abundance of the prey but by other factors. The high populations of Coccinellids of Plot C were ascribed to its situation between the two nettle sites, Great Field II and Great Field III, with their large populations of ladybirds; the comparatively small coccinellid populations of Plots A and D were associated with the distance of these plots from places harbouring ladybirds; at Plot A, the surrounding trees and buildings probably hindered the ladybirds from reaching the plot.

Estimation of Mortality Rates of Coccinellids on the Bean Plots.

Mortalities of the immature stages of Coccinellids on the bean plots at particular times have already been mentioned; cannibalism at Plot C was responsible for the large loss of just-hatched larvae in weeks 9 and 10 and, on

Plot D, the feeding problems confronting large numbers of larvae of the second phase have been stressed.

It is not possible to link the numbers of adult Coccinellids at the beginning with those at the end of the infestations owing to the complications arising from emigration and immigration; but it is possible to estimate approximately the mortalities between various stages from eggs to pupae and to attempt an explanation of any differences between plots.

Estimates of the actual numbers of individuals of any one stage on any one day may be obtained by dividing the total number counted on a plot during the period of 8 or 9 weeks by the duration of that stage. From these figures, the mortality from stage to stage may be estimated and thus the proportion surviving. The results have been obtained in a similar fashion for each plot and may be compared.

The durations of the various stages adopted for these estimations are as follows (see p. 576): egg stage, 7 days; just-hatched larva, 0·5 day; "missing stage", 7 days; older larva, 14 days; pupa, 9 days. The durations of the stages, which are considered representative for all the species, would probably vary from time to time.

Corrections for the fauna in the litter on the last sampling occasions (from Table X) have been applied to the totals of Coccinellids counted during the weeks 7–15 (from Table III) and these new totals have been divided by the durations of the stages to give the estimated populations for each plot and the mortality rates therefrom (Table XI).

Eggs—just hatched larvae.

Between these stages, mortalities were identical on Plots C and D but considerably lower on Plot A.

There was no pronounced infertility of the eggs, and no extensive destruction of just-hatched larvae was observed. While egg destruction by cannibalism is suggested as a possible contributory cause of the high mortality of Plot C, no satisfactory explanation for the identical loss on Plot D or the lowness of the mortality on Plot A can be advanced.

Just-hatched—older larvae.

On Plot A, Aphids and other food (*e.g.*, coccinellid eggs) were comparatively scarce, especially in the early stages of the aphid infestation, but on Plots C and D, where Aphids were very abundant, mortality rates were almost as high as on Plot A and a shortage of food was probably not the main cause of mortality. There are two other possibilities, both functions of prey density, (1) the difficulty of young larvae in finding the aphid colonies, (2) the large amount of honeydew on the heavily infested plants might hinder feeding and development of the young larvae.

Older larvae—pupae.

Mortalities in these stages were caused apparently by birds. Sparrows (*Passer domesticus*) occurred especially at Plots A and C and at the former four robins (*Erithacus rubecula*) were constantly present. At these two plots numbers of half-eaten pupae were found during the last two weeks of the surveys. At Plot A during the summer of 1953, when larvae tagged with radioactive labels were being studied (Banks, 1954*b*), robins were again present and were held responsible for the loss of several larvae. One robin was captured but was not radioactive; however, one of many masses of bird-droppings near the plot was highly radioactive.

Cannibalism and predation by birds cannot explain all the larval mortality observed and while a shortage of food was probably an important cause at certain times, recent work (Banks, *l.c.*) suggests that many young larvae die of starvation and exhaustion before encountering a food supply on account of the ineffectiveness of their searching behaviour and of the oviposition habits of the adult insects.

Discussion.

The potentialities of the overwintered Coccinellids were not directed entirely against *Aphis fabae* but partly against *Microlophium evansi* on nettles; consequently, populations of *A. fabae* were able to start developing on the beans without large populations of adult and larval Coccinellids to attack them.

On Plot C, where large numbers of ladybirds arrived and laid many eggs when the aphid population was still low, the larvae did not attack the Aphids so readily as they did the unhatched coccinellid eggs. Again, the nettle brood at Plot D laid large numbers of eggs when the Aphids had already reached their maximum density and were about to decline; many of the resulting larvae probably died of starvation for the aphid numbers had fallen almost to zero. Finally, the Coccinellids of the bean brood reached the adult stage by the time that the aphid infestations were over.

The effectiveness of the Coccinellids as predators of *A. fabae* was, therefore, reduced, partly by the arrival of the Aphid on the beans when the overwintered Coccinellids had already emerged from hibernation and partly by the availability of an alternative prey on nettles. To be effective against a polyphagous Aphid like *A. fabae*, any insect enemy would have to attack it on all its host-plants. The effectiveness of predators has been discussed by Varley (1953).

Other authors have emphasised the importance of alternative prey in reducing the effectiveness of a parasite or predator against a particular species (Leopold, 1933; Solomon, 1949; Allee & others, 1949); but the effectiveness is even more reduced if the alternative prey is in a separate habitat, as *Microlophium* was. *M. evansi*, though acting as a " buffer " in diverting the force of the coccinellid attack against *A. fabae*, was, however, a first food supply for the predators recently emerged from hibernation and was probably important for their survival (Leopold, *l.c.*, p. 237).

While some species of Coccinellids are specific in their food habits (Thompson, 1929), aphid-eating members of the family are not restricted to any one species of Aphid for their main food supply (Schilder & Schilder, 1928; Clausen, 1940) and Clausen (p. 573) remarks " In the aphid- and scale-feeding species particularly, there is often a pronounced tendency to vary the diet, and many species will be found to feed at times upon immature stages of Lepidoptera, Hemiptera, etc. Some have been shown to feed extensively at nectar glands of plants and on sap, pollen, fungi, honeydew, etc." The Coccinellids considered in this survey have been recorded as predators of many aphid species (Schilder & Schilder, *l.c.*; Smee, 1922; Smith, 1931).

The abundance of a predator is usually associated with the abundance of its prey (Allee & others, *l.c.*, p. 374); while this is probably true from year to year the present results indicate, when all three plots are considered, that the numbers of adult Coccinellids which came to the plots were not dependent on the abundance of the Bean Aphids but either on the proximity of a plot to nettles harbouring ladybirds, or the remoteness of a plot from such places, or the shelter afforded by trees and buildings which hindered the access of the beetles to the beans. Fenjves (1945) remarked on the influence of surrounding vegetation on the population of coccinellid larvae on a potato field in Switzerland; in one field close to a wood where Coccinellids were numerous, there was a population of 0·4 larvae per plant as against 0·1 larvae per plant elsewhere. Heinze & Profft (1940) noted the effect of sudden immigrations of adult Coccinellids on to potato fields in Germany in 1936 and 1937.

The abundance of coccinellid eggs and larvae of the bean plots depended on the numbers of adult Coccinellids which came to the plots and was not correlated with the density of the Aphids there; nor is there any evidence of a correlation between the survival rates of the various immature stages and the densities of the Aphids of the plots.

Although the adult and larval Coccinellids attacked the Bean Aphids and reduced their numbers, their effect was not noticeable and the populations of the predators apparently varied independently of those of the Aphids. Under other circumstances, Coccinellids might be effective against an abundant polyphagous Aphid like *A. fabae* if they could concentrate their attack on the one species of Aphid as soon as it arrived on its host-plant.

Summary.

Changes in numbers of adult Coccinellids on nettles infested with *Microlophium evansi* (Theo.) and on three experimental bean plots infested with *Aphis fabae* Scop. are described for the spring and summer of 1952 at Rothamsted. Of the three common species, *Adalia bipunctata* (L.), *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.), the first was always the most abundant.

The overwintered Coccinellids produced two broods: one on nettles in the spring and one on beans in early summer.

On bean plots, changes in numbers of the adult insects occurred in three phases: (1) overwintered ladybirds, dispersing from nettles and other places, accumulated on the beans in the early stages of the infestations by *Aphis fabae*; (2) ladybirds, which had developed from eggs laid by the overwintered insects on nettles, emigrated from nettles and accumulated on the beans when *A. fabae* populations were at their height; (3) ladybirds, developed from eggs laid on the beans also by the overwintered insects, reached the adult stage when the bean aphid infestations had finished. The rise and fall of the *A. fabae* populations are discussed.

One of the bean plots had always a high population of Coccinellids, which was attributed to its situation between two of the nettle sites. The other two bean plots were remote from nettles and one was sheltered by trees and buildings; their coccinellid populations were much lower.

Variations in numbers of coccinellid eggs and larvae on the bean plots followed those of the adult insects both in phase and in numbers, with the exception that there was no third phase of eggs and larvae to correspond to that of the adults.

Cannibalism (destruction of eggs by larvae) was frequently observed on the bean plot with the high coccinellid population, where, in one week, a loss of about 56 per cent. of newly-hatched larvae was attributed to cannibalism. The evidence suggests that cannibalism was caused partly by a scarcity of Aphids but chiefly by an abundance of eggs and was also influenced by the relative locations of egg batches and of Aphids on the stems; larvae dispersing from the egg shells after hatching probably encountered egg batches on the lower leaves more readily than the Aphids at the tops of the plants.

A very high aphid population was responsible for the early defoliation of the plants on another bean plot and for the consequent accumulation of much of the predator fauna in the ground litter. Many coccinellid larvae from the numerous eggs laid during the second phase probably died of starvation towards the end of the infestation owing to the disappearance of many of the Aphids.

The numbers of coccinellid eggs and larvae of the different plots did not depend on the sizes of their aphid populations but on the numbers of adult Coccinellids coming on to the beans; and the mortality rates of the immature stages were apparently not correlated with the aphid densities of the three plots.

The main factors determining the numbers of adult Coccinellids of the bean plots appeared to be the distance of the plots from nettles harbouring ladybirds and the shelter afforded by trees and buildings.

Coccinellids were ineffective as predators of *A. fabae* because the majority of the overwintered ladybirds and their progeny were already attacking *M. evansi* on nettles when *A. fabae* arrived on the beans. When many Coccinellids did arrive on the beans, the aphid infestations there had already reached their maximum numbers and the effectiveness of these predators was again reduced.

Acknowledgements.

It is a pleasure to thank Dr. C. B. Williams, F.R.S., Professor G. C. Varley and Dr. C. G. Johnson for their interest in this work and for many stimulating discussions. I am also much indebted to Mr. M. E. Solomon for his helpful criticism of the typescript. Mrs. C. P. Jenkins has given valuable help in the field and in the laboratory.

References.

Allee, W. C., Emerson, A. E., Park, O., Park, T. & Schmidt, K. P. (1949). Principles of animal ecology.—837 pp. Philadelphia, Saunders.

Banks, C. J. (1954*a*). Random and non-random distributions of Coccinellidae.—J. Soc. Brit. Ent., **4,** pp. 211–215.

Banks, C. J. (1954*b*). The searching behaviour of Coccinellid larvae.—Brit. J. Anim. Behav., **2,** pp. 37–38.

Banks, C. J. (1954*c*). A method for estimating populations and counting large numbers of *Aphis fabae* Scop.—Bull. ent. Res., **45,** pp. 751–756.

Clausen, C. P. (1940). Entomophagous insects.—688 pp. New York, McGraw-Hill.

Fenjves, P. (1945). Beiträge zur Kenntnis der Blattlaus *Myzus* (*Myzodes*) *persicae* Sulz., Überträgerin der Blattrollkrankheit der Kartoffel.—Mitt. schweiz. ent. Ges., **19,** pp. 489–611.

Heinze, K. & Profft, J. (1940). Ueber die an der Kartoffel lebenden Blattlausarten und ihren Massenwechsel im Zusammenhang mit dem Auftreten von Kartoffelvirosen.—Mitt. biol. Reichsanst., no. 60, 164 pp.

Johnson, C. G. (1950). A suction trap for small airborne insects which automatically segregates the catch into successive hourly samples.—Ann. appl. Biol., **37,** pp. 80–91.

Leopold, A. (1933). Game management.—481 pp. New York, C. Scribner's Sons.

Nicholson, A. J. (1933). The balance of animal populations.—J. Anim. Ecol., **2,** pp. 132–178.

Schilder, F. A. & Schilder, M. (1928). Die Nahrung der Coccinelliden und ihre Beziehung zur Verwandtschaft der Arten.—Arb. biol. Reichsanst., **16,** pp. 213–282.

Smee, C. (1922). British ladybird beetles. Their control of Aphids.—Fruit-grower, **53,** pp. 675–676, 717–718, 759–760.

Smith, K. M. (1931). A textbook of agricultural entomology.—285 pp. Cambridge, Univ. Press.

Solomon, M. E. (1949). The natural control of animal populations.—J. Anim. Ecol., **18,** pp. 1–35.

THOMPSON, W. R. (1929). On the relative value of parasites and predators in the biological control of insect pests.—Bull. ent. Res., **19,** pp. 343–350.

THOMPSON, W. R. (1939). Biological control and the theories of the interactions of populations.—Parasitology, **31,** pp. 299–388.

ULLYETT, G. C. (1953). Biomathematics and insect population problems. A critical review.—Mem. ent. Soc. S. Afr., no. 2, 89 pp.

VARLEY, G. C. (1953). Ecological aspects of population regulation.—Trans. IXth int. Congr. Ent., **2,** pp. 210–214.

EXPERIMENTS IN TSETSE CONTROL IN SOUTHERN TANGANYIKA.

By E. Bursell

East African Tsetse and Trypanosomiasis Research and Reclamation Organisation, Central Tsetse Research Laboratory, Shinyanga, Tanganyika Territory.

During the period October 1951 to October 1953 a survey was made of a recent spread of *Glossina morsitans* Westw. in the Songea District of southern Tanganyika. Since October 1953, observations have been continued by African Assistants under the supervision of the Provincial Tsetse Officer, Department of Tsetse Survey and Reclamation, Tanganyika Territory, and it has been possible to include data collected up to July 1954.

The main features of the invasion are illustrated in the map (fig. 1). The first symptoms were noted in 1941 when cattle started dying of trypanosomiasis at Gumbiro. Flies spreading from the main body of the eastern fly-belt, some 20 miles east of Gumbiro, had reached the area in sufficient numbers to effect permanent settlement of an extensive tract of woodland between Gumbiro and Songea township.

In 1947 an outbreak of trypanosomiasis occurred about 15 miles farther west; the flies had been able to bridge the cultivation belt lying between Gumbiro and

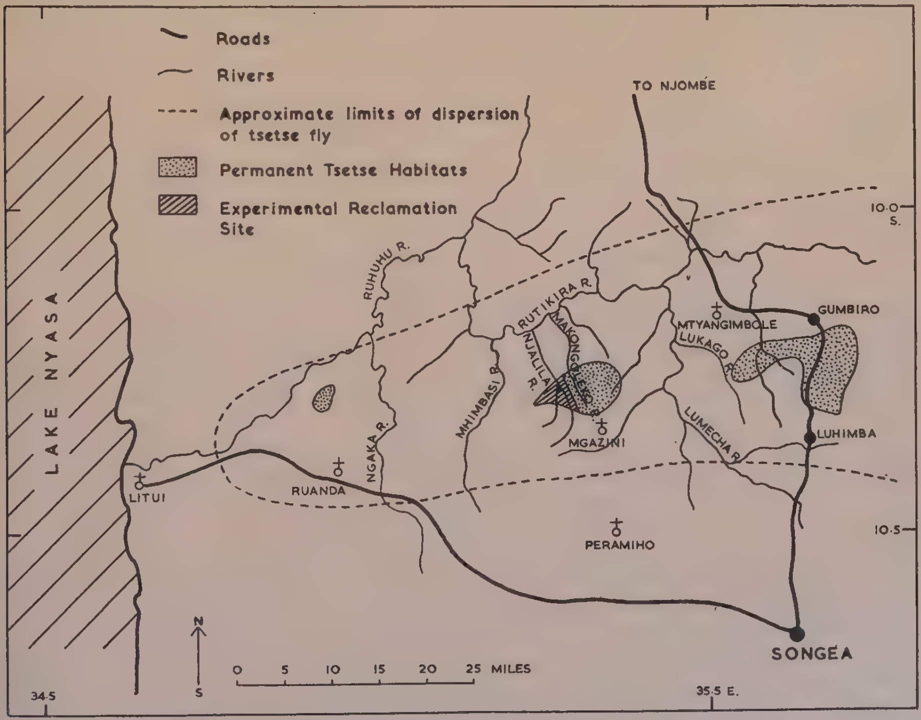

Roads
Rivers
Approximate limits of dispersion of tsetse fly
Permanent Tsetse Habitats
Experimental Reclamation Site
TO NJOMBE
10.0 S.
LAKE NYASA
RUHUHU R.
RUTIKIRA R.
NJALILA R.
MAKONGOLESO R.
MHIMBASI R.
NGAKA R.
MTYANGIMBOLE
LUKAGO
GUMBIRO
LUHIMBA
LUMECHA R.
MGAZINI
LITUI
RUANDA
PERAMIHO
10.5
SONGEA
N
S
0 5 10 15 20 25 MILES
34.5
35.5 E.

Fig. 1.—Map showing the area recently invaded by tsetse fly in Songea.

a tract of woodland centred on the Katumbakawana hills, near Mgazini, and a permanent population had become established there.

The last stage of this westward spread occurred during 1953, when a wooded escarpment near the shores of Lake Nyasa was invaded by flies spreading from the Mgazini infestation.

Apart from delimiting the extent of the recent invasion, the object of the present survey was to determine the relation between the tsetse and its environment in the invaded areas, and if possible to formulate and test methods of eradication.

Methods.

To determine the distribution of flies and seasonal fluctuations in population density, fly-rounds were laid out in representative parts of the salient. These were generally 3–4 miles long and divided into sectors of 100 yd. which were numbered consecutively. Two pairs of traverses were made monthly, the first of each pair with the catchers starting at the first sector and proceeding to the last, the second in the reverse direction and two days later. Population densities are expressed as Apparent Density (A.D.) which is the number of male non-teneral flies caught per 10,000 yd. of fly-round. The relation between this measure and the actual population is not known, but recent work in East Africa indicates that changes in A.D. reflect changes in population density fairly closely. The results are presented with this qualification.

The hunger of flies was estimated by the method of Jackson (1933) and the number of hungry (Stage 4) and replete (Stage 2) flies is expressed as a percentage of the male non-teneral catch.

Pupal surveys were carried out to test conclusions reached by consideration of fly densities. Selected sites (fallen logs of wood, rot-holes, overhanging rocks, etc.) were searched in representative parts of the area, and results were expressed as the number of full and/or empty puparia per sq. yd. of site searched.

Results.

The climate of Songea.

The year may conveniently be divided into four parts on the basis of climatic differences in Songea:—

(i) The early rains (November–December).

These begin in November and may or may not be separated, by a very short dry season in December, from

(ii) The long rains (December–April).

The long rains continue until the end of April. Mean temperatures during these two seasons fall steadily from 74°F. in November to 70°F. in April. Saturation deficiencies are low except during November. The mean monthly rainfall is about 7 in.

(iii) The cool dry season (May–August).

This season is characterised by rapidly falling temperatures which reach a minimum of about 65°F. in July and August. The saturation deficiency, which is high in April and May, shows a corresponding fall in July and August.

(iv) The hot dry season (September–October).

During this period temperatures rise rapidly to 74°F. in October; the saturation deficiencies are high throughout this season.

The mean monthly rainfall during the dry season is 0·2 in.

The vegetation of the invaded areas.

The areas which have recently been invaded by tsetse appear to have been well populated during the last century; from local evidence it seems that they were deserted about the time of the Maji-Maji rebellion, early in the present century. Owing to the somewhat primitive methods of cultivation practised in these parts of Songea, conditions for regeneration would be favourable once the cultivations had been abandoned. The original vegetation has been able to re-establish itself without reverting to earlier stages in the plant succession, and at present the vegetation has reached the dry sub-climax characteristic of the greater part of southern Tanganyika. This sub-climax is the *Brachystegia-Pseudoberlinia* woodland, locally known as " miombo ". In the areas under consideration the dominant species are *Brachystegia floribunda*, *B. bussei*, *B. boehmii* and *Pseudoberlinia globiflora*. These trees are usually from 30–50 ft. in height and form a more or less continuous canopy. They are associated with a number of lower-storey elements, the most important genera being *Diplorhynchus*, *Pseudolachnostylis*, *Dichrostachys*, *Ochna*, *Combretum* and *Uapaca*.

The miombo is in many places broken by extensive glades, usually along the tops of ridges. These glades support a different plant community, with shrubs like *Piliostigma thonningii* and *Acacia* spp. as characteristic elements, and large trees like *Albizzia* sp. representing relicts of a former forest climax, left by the original settlers perhaps as shade trees. I am indebted to Mr. A. G. H. Du Frayer of the Department of Tsetse Survey and Reclamation, Tanganyika Territory, for pointing out that these glades represent old village sites, as evidenced by the remains of domestic utensils which can always be found in them. It seems likely that severe compaction of the soil in these areas has precluded invasion by the surrounding miombo. The interzone between glade and woodland is characterised by a well-marked double canopy; the development of second-storey elements here has presumably been favoured by better conditions of light and lessened competition in the ecotone. The interzone is nearly always short-grassed, while in the glade itself stands of tall *Hyparrhenia* are often found.

The continuous canopy of the miombo is also broken near some of the larger drainage lines, by the occurrence of open, tall-grassed seasonal swamps called " mbugas ". These are bounded on the one hand by riverine forest, and on the other by the ridgeside miombo; but in this case a double-canopied interzone is not usually well developed.

The ecology of the tsetse.

(i) *The distribution of flies along the fly-rounds.*—Results from the four main fly-rounds show clearly that peaks in population density are associated with the open ridgetop glades. The data from one of the fly-rounds are summarised in fig. 2 (a, b). These peaks are particularly marked in the dry season when A.D.s in or near the glades are 3–5 times as high as in the surrounding woodland. In the wet season the flies are more evenly distributed and glade A.D.s are only twice as great as the A.D.s in the general miombo.

The invariable association of high A.D.s with ridgetop glades suggests that these breaks in the miombo constitute the preferred habitat or concentration areas of the tsetse.

It was not possible to get a clear-cut confirmation of this conclusion from a consideration of the differential distribution of hunger stages and of females. The glades are often quite small, so that the catch from a single sector of the fly-round was drawn partly from the concentration area and partly from the surrounding woodland. But in general terms it was found that female percentages were lower near the concentration areas than in the general woodland; the percentage of hungry flies also was lower, while the Stage 2 percentage was usually higher. Low Stage 4 and female percentages and high percentages of Stage 2 are generally regarded as indicating a healthy population, so these tendencies lend some support to the conclusion that ridgetop glades constitute the concentration areas of the fly.

But they stand in such marked contrast to findings in other parts of the territory that it was thought necessary to extend the observations. For this purpose three small fly-rounds were set out in association with a single large concentration area; one sampled the open glade only, one the interzone only and one the homogeneous woodland about 200 yd. away from the interzone. These fly-rounds were done on three different days with a day's interval between each, the whole repeated once every two weeks. The fly-rounds were constructed immediately before my departure from Songea and during the last nine months observations have been carried out by a team of African fly-boys. The results to date are summarised in Table I, and illustrated in fig. 2,d where hungry (Stage 4, females and tenerals) and replete (Stages 1 and 2) flies have been plotted.

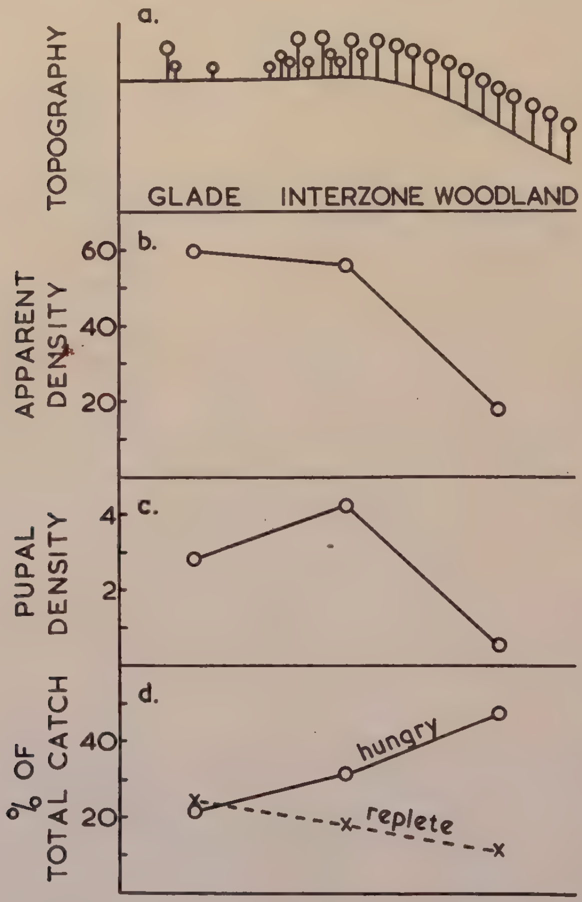


Fig. 2.—The distribution of flies and pupae in different parts of the environment.

These results show very clearly the preponderance of hungry flies in the woodland and of replete flies in the concentration area. In other parts of Tanganyika the situation is the exact reverse, with the highest proportion of hungry flies and females in the open mbuga and the highest proportion of replete flies in the woodland (Jackson, 1930). This latter distribution has given rise to the concept of feeding ground (see also Nash, 1930) and it follows that this theory is not applicable to the situation in Songea. It remains to be discovered whether this difference reflects differences in behaviour of the fly or differences, as yet undefined, in the pattern of its habitat, or both.

In the mbugas, flies may be caught in considerable numbers after the grasses have been burnt in August or September; but as soon as the grasses reach full development again, the flies disappear almost completely.

TABLE I.

The differential distribution of hunger stages, females and tenerals in different parts of the environment.

Area sampled	Glade	Interzone	Woodland
A.D.	60	56	18
Stage 1 (%)	14·3	4·5	16·7
„ 2 (%)	10·7	14·9	0
„ 3 (%)	65·5	58·2	50·0
„ 4 (%)	9·5	22·4	33·3
Female (%)	12·5	9·4	21·7
Teneral (%)	1·0	2·6	0

Pupal surveys were carried out in conjunction with three of the fly-rounds and served to confirm the importance of the ridgetop glades. These had pupal densities of 2·8 in the open and 4·2 in the interzone between glade and miombo, as compared with a value of 0·6 for the ridgeside woodland (see fig. 2,c); the density in and near mbugas was 1·8.

These results suggest that the ridgetop glades are of vital importance in the economy of the Songea tsetse, and that an attack on these sites would interfere with breeding as well as with other aspects of tsetse ecology.

(ii) *Seasonal fluctuations in A.D. and in population composition.*—A well-marked seasonal cycle was characteristic of the results from all four fly-rounds. The data for the Gumbiro round are shown in fig. 3. The main features of the cycle are an increase in population density starting in January or February,

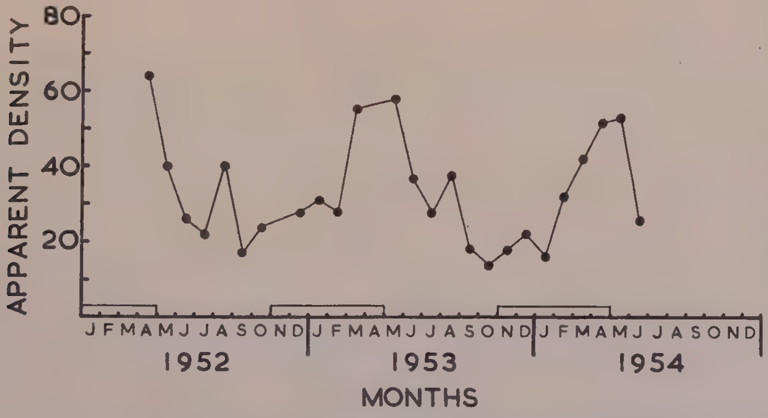


Fig. 3.—Seasonal fluctuations in apparent density. The rainy seasons are marked on the abscissa.

about two months after the onset of rains, with high A.D.s during the remainder of the rainy season, falling in the early dry season. There is a partial recovery in August, perhaps associated with the low temperatures and correspondingly low saturation deficiencies, with a drop to a second trough in September and

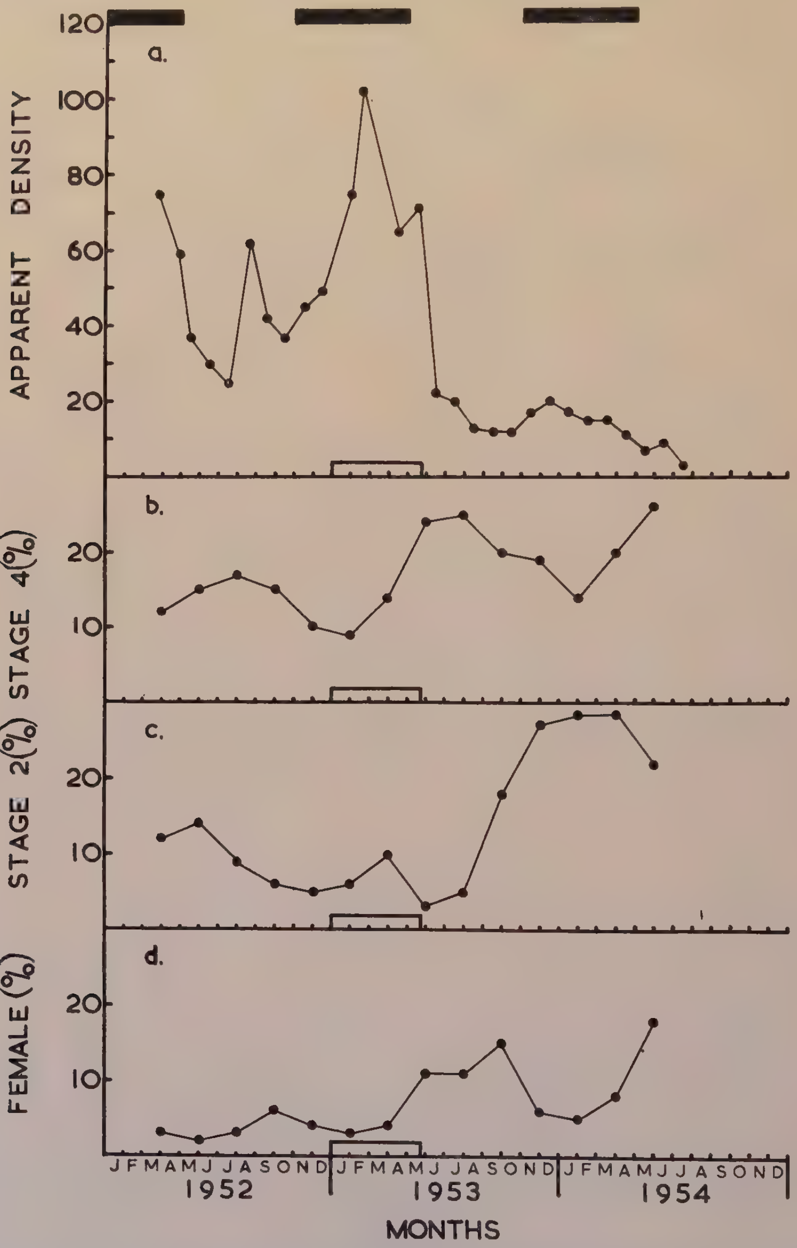


Fig. 4.—The effect of discriminative clearing on fly density and population composition. The period during which clearing was in progress is marked on the abscissa, and rainy seasons are shown at the top of the figure.

October. The cycle thus shows a rough negative correlation with saturation deficiency.

The Gumbiro round serves as a control round for the experimental reclamation scheme (see below) and it is of particular significance that the August peak occurred both in 1952 and in 1953, and that recovery of the population after the dry season took place in 1954 as well as in the previous years.

Associated with these changes in A.D. are changes in the population composition (illustrated in the left-hand third of fig. 4 (1952) for the Njalila fly-round before discriminative clearing was begun). In general terms, Stage 4 percentages are higher during the dry season than during the rains; Stage 2 percentages are high during the late rainy and the cool dry seasons and female percentages are highest in September and October, when saturation deficiencies are maximal.

Discriminative clearing.

The invariable association of high fly densities with a well-defined vegetation complex, the ridgetop glade, suggested that discriminative clearing would prove a suitable method of reclamation. One of the most characteristic features of the preferred habitat is the well-developed double canopy in the interzone between woodland and glade. It was thought that this ecotone might be of special significance for the fly, and that sufficient interference with it would render the habitat unsuitable and lead to eventual extermination of the tsetse.

To test this possibility and to determine the degree of interference which would be necessary to produce the desired result, an experimental reclamation scheme was started. The site chosen was an area of about 14 square miles, centred on the Njalila and Mtungurusi rivers, at the westernmost tip of the Mgazini infestation. This region is bounded, on three sides, by country unsuitable for tsetse; to the north and west by the plains of the Rutikira and Mhimbasi river valleys, and to the south by the Lihange mountains and by cultivations. Invasion by flies could occur only from the east, across the Makongoleko river; but since a stretch of heavily dissected country with rather sparse woodland is interposed between the reclamation site and the nearest concentration areas east of Makongoleko it was hoped that the rate of invasion would not be great enough to obscure the effect of clearing on population density.

The experimental site was treated as three blocks separated by the two permanent rivers. In the western block, only the lower canopy of the interzone was cleared; in the eastern block, only the upper storey elements were cut down, while in the central block the whole of the interzone was cleared. The work was started in January 1953 and completed in April.

The fluctuations in population density and composition before and after clearing of the experimental site are shown in fig. 4. The clearings were completed at a time when A.D.s were dropping at the end of the 1953 rains. The secondary peak which is imposed on the decline during 1953 was probably due to flies migrating from concentration areas in the process of being cleared and not sampled by the fly-round to areas already cleared on the fly-round itself. During June and July there is no difference between 1952 and 1953 A.D.s, but the effect of the treatment is reflected in a marked increase in percentage of hungry flies and a decrease in the Stage 2 percentage (fig. 4, b, c). In August and September the effect on fly numbers becomes evident; the population has been unable to recover to the normal August peak, and A.D.s remain at very low levels. Nor is there any sign of recovery to normal A.D. after the onset of rains, so that A.D.s during the early part of 1954 are only about 10 per cent. of the 1952 and 1953 values. The Stage 4 percentage and the female percentage have remained well above pre-treatment values ever since clearing was completed, but the Stage 2 percentage, after the initial depression, has shown a remarkable increase. The significance of this increase is not clear, but it evidently does not indicate a real recovery on the part of the population, since A.D.s have remained low.

It has been mentioned that an invasion of the experimental block from the east was to be expected. To gauge the extent of this invasion, flies have been marked on the ridge east of the Makongoleko river during the last months of 1953 and the first half of 1954, and recaptures within the experimental site noted. The results are shown in Table II.

TABLE II.

Recaptures in the experimental block of flies released east of the Makongoleko river.

Month		Mean daily catch Makongoleko East	Percentage recaptures included in the total catch	
			In marking area	In experimental block
October	1953 ..	9	0	0
November	,, ..	11	5·3	2·0
December	,, ..	14	3·7	1·5
January	1954 ..	23	5·7	7·5
February	,, ..	22	8·9	9·5
March	,, ..	29	14·8	0
April	,, ..	26	13·8	0
May	,, ..	20	15·5	8·0
June	,, ..	14	14·2	7·5
July	,, ..	12	9·0	0

It is seen that from November till February the percentage recaptures at Njalila and at Makongoleko were roughly on the same level, indicating that a very large proportion of the flies caught at Njalila were migrants from concentration areas outside the reclamation site. Towards the end of the rains the percentage recaptures in the marking area increased greatly while at Njalila few recaptures have been made since February. This may indicate that with the onset of unfavourable climatic conditions the rate of dispersal from Makongoleko concentration areas has decreased; if that were so a further drop in the A.D. at Njalila would be expected during the early dry season, and such a drop has indeed occurred (see fig. 4,a).

Table II also shows that, as at Gumbiro, so in the area adjoining the experimental block, a normal recovery of the population took place during the 1954 rains; the mean daily catch increased threefold. So the collapse of the population at Njalila may be safely attributed to the effect of discriminative clearing.

It seems permissible to conclude that complete success of discriminative clearing is being obscured by immigration from concentration areas outside the reclamation block, and that in the absence of such immigration the population would die out completely; in other words, that discriminative clearing will prove an effective means of eradication in Songea.

Separate consideration of A.D.s from the three differently treated blocks does not as yet permit a decision as regards the relative merits of the three types of clearing. All have been effective in reducing the population to very low levels, and in none of the regions has a population been able to recover during the 1954 rains. But there is a possibility that lower-storey clearings will regenerate fairly quickly to reconstitute a habitat suitable for tsetse. Already, towards the end of 1953, regeneration was well established, and shade conditions in the interzone were if anything better than they were before clearing. But shade, clearly, is not the only important factor, and up till now (15 months after treatment) the clearings have proved incapable of supporting a normal population.

Whatever the long-term outcome of lower-canopy clearing will turn out to be, there can be no doubt of the efficacy of upper-canopy clearing; here the danger of a suitable habitat being reconstituted within a reasonable number of years (say 20) is very remote.*

Summary.

A recent extension of the fly-belt in Songea, southern Tanganyika, has been delimited.

The preferred habitat of the tsetse in this region is constituted by open, short-grassed glades, representing old village sites, in well-grown *Brachystegia* woodland, with a double-canopied interzone between glade and woodland.

Destruction of this interzone by clearing of the upper canopy will undoubtedly prove effective in causing eradication of the fly.

Acknowledgements.

This work was carried out under the supervision of the East African Tsetse and Trypanosomiasis Research and Reclamation Organisation while the author was employed as Tsetse Officer by the Provincial Administration, Southern Province, Tanganyika Territory. He is indebted to the Provincial Commissioner, Southern Province, and to the Director, E.A.T.T.R.R.O., for permission to publish this paper, and also to members of the staff of E.A.T.T.R.R.O., particularly to Mr. A. G. Robertson and Mr. R. D. Pilson, for valuable discussion.

References.

Jackson, C. H. N. (1930). Contributions to the bionomics of *Glossina morsitans*.—Bull. ent. Res., **21**, pp. 491–527.

Jackson, C. H. N. (1933). The causes and implications of hunger in tsetse-flies.—Bull. ent. Res., **24**, pp. 443–482.

Nash, T. A. M. (1930). A contribution to our knowledge of the bionomics of *Glossina morsitans*.—Bull. ent. Res., **21**, pp. 201–256.

---

* During the last half of 1954 and the first two months of 1955, February being the last month for which data are available, A.D.s on the experimental reclamation fly-round have been between 3 and 5.

THE EFFECT OF PHOTOPERIOD AND TEMPERATURE ON REPRODUCTION IN *ACYRTHOSIPHON PISUM* (HARRIS) AND ON THE FORMS PRODUCED.

By Joyce Kenten

Department of Insecticides and Fungicides, Rothamsted Experimental Station, Harpenden, Herts.

(Plate XIX.)

Most species of Aphids occur in a number of different forms, parthenogenetic (*e.g.*, apterous and alate virginoparae, gynoparae, fundatrices) and sexual (oviparae and males). The available evidence suggests that external factors to a large extent determine which forms are found in a population. The early work of Marcovitch (1923, 1924) and Davidson (1929) demonstrated that photoperiod and temperature can influence the presence or absence of the sexual phase in Aphids and these results have been confirmed by the work of Bonnemaison (1951), de Fluiter (1950) and others. It has been claimed by Shull (1929, 1942) and White (1946) that photoperiod and temperature can also influence the proportion of apterae and alatae found in a population, but Bonnemaison (1951) has failed to repeat some of the observations on which these claims were based.

There is evidence suggesting that other factors can influence aphid form, for example Bonnemaison (1951) claims that the species of the host plant, and the proximity of one Aphid to another (the effect of the group), influences the proportion and type of sexual forms found in a population; while the majority of the experimental evidence suggests that the production of alate virginoparae is influenced most strongly by factors connected with overcrowding and starvation (for example Gregory, 1917; Wadley, 1923; Reinhard, 1927; Davidson, 1929; Rivnay, 1937; Smith, 1937; Schaefer, 1938; and Bonnemaison, 1951). In the present work, only the factors of photoperiod and temperature have been examined and other factors have been kept as uniform as possible.

The Aphid studied was the Pea Aphid, *Acyrthosiphon pisum* (Harris), an Aphid frequently used as a test insect in the study of insecticides.

Materials and Methods.

In the experiments described, a preliminary study has been made of the effect of photoperiod and temperature on the production of the various forms of *A. pisum*. This study has been limited to the treatment of apterous virginoparae and no other forms; exposure to the different photoperiods and temperatures was confined as far as practicable to a single parent generation. Parent apterae (which were the offspring of Aphids which had been reared under standardized conditions of temperature and photoperiod for many generations prior to the experiments) were exposed throughout their life to two photoperiods and six different temperatures. The offspring produced by these Aphids were collected at intervals and kept until maturity under the standard conditions of photoperiod and temperature used to condition the stock; their form was then determined and the effect of the various treatments assessed.

In an attempt to discover whether the duration of a stimulus and the stage at which it was applied to a parent aptera affected the type of offspring it produced, a slight elaboration was made to the experimental technique. The life of the parents was divided into two stages, the nymphal period from birth until the last imaginal moult, and the adult period from the last (imaginal) moult until death, and the photoperiod treatments received during these two stages were varied in such a way that four treatments were obtained:

(1) Parents which received a photoperiod of 8 hr./24 hr. throughout their life.

(2) Parents which received a photoperiod of 8 hr./24 hr. during their nymphal period but 16 hr./24 hr. during their adult period.

(3) Aphids which received a photoperiod of 16 hr./24 hr. during their nymphal period, and 8 hr./24 hr. during their adult period.

(4) Aphids which received 16 hr./24 hr. throughout their entire life.

Experimental cages.

Six experimental lightproof cages were set up. Each cage was lit by one 15-Watt clear tungsten bulb placed over a pneumatic trough filled with distilled water. The illumination period of each bulb was controlled by a time switch, and at each of the temperature conditions one cage was illuminated for 8 hours and the other for 16 hours in every 24 hours. The desired temperatures were obtained by placing the cages in thermostatically controlled cabinets. Six different temperatures were used, 29–30°C., 25–26°C., 19–20°C., 11–13°C., 7–11°C. and 5–9°C. The maximum temperature variation was ± 2°C. Humidity was not controlled but measurements suggest that over the whole temperature range it was between 60 and 90 per cent. in the neighbourhood of the Aphids.

Plant material.

Broad bean plants (*Vicia faba*) of the variety Seville Longpod were grown in 3 in. pots in John Innes compost, three beans to each pot. The plants were kept at a constant temperature of 19–20°C., and continuously illuminated by a dim light. They were used in the experiments when the shoots were between ½ to 3 in. high.

Standard Aphid culture.

Approximately six months before the start of the experiments, a number of adult apterous virginoparae of *A. pisum* were placed on young bean shoots, approximately 3 ft. beneath two 80-Watt fluorescent tubes. The temperature was maintained between 19 and 20°C., and the lighting was continuous. From the descendants of these Aphids, a culture, subsequently referred to as "standard Aphids", was maintained under these conditions of light and temperature in the following manner:—

One to two days after their last (imaginal) moult 8 to 11 adult apterous virginoparae were placed on young broad bean shoots (½ to 3 in. above soil level) and covered with a hurricane lamp glass with its open end covered by a piece of muslin. These adults were left to reproduce on the plants for one to two days and then discarded. The offspring when mature were used to perpetuate the "standard" stock as described. It was found that under these conditions sexual forms were never produced and alate virginoparae and apterous virginoparae bearing sensoria on the hind tibiae occurred only rarely.

Thus successive batches of standard Aphids were obtained with the following characteristics:—

They and their ancestors (for a large number of generations) had been reared under constant conditions of temperature and light.

They were the product of a long line of apterous virginoparous ancestors.

They became adult at approximately the same time.
They were the offspring of parents of approximately the same age.

Examination of Aphids.

Aphids to be examined were covered with lactic alcohol (70% lactic acid and 70% alcohol 1:1), warmed over a water bath for 10 to 15 minutes, then the lactic alcohol was poured off and the Aphids covered with liquefied phenol. When the specimens had cleared they were examined individually through a binocular microscope at a magnification of × 8.

Aphid types.

Four main forms of *A. pisum* were produced by the experimental treatments:—

Apterous virginoparae (Ap ♀)
Alate virginoparae (Al ♀)
Males (♂) (All the males produced in these experiments were alate.)
Oviparae (♀).

It was found, however, that under certain conditions a variety of forms intermediate in character between the apterous virginoparae and the oviparae were obtained. These were classified in the following manner:

(a) Individuals which possessed sensoria on the hind tibiae (a normal characteristic of oviparae), but which contained embryos and not eggs. These were placed in a separate class known as apterous virginoparae bearing sensoria (Ap ♀ + s). No note was made of the number of sensoria present although this was found to vary from one on one leg to many on both (Pl. XIX, fig. 1). It was rare, however, to find in these forms the short thickened hind tibiae bearing many sensoria, which are typical of oviparae (Pl. XIX, fig. 2).

(b) Individuals which contained eggs were classed as oviparae even though they possessed few or no sensoria on the hind tibiae, or contained embryos as well as eggs (Pl. XIX, fig. 3). Individuals which contained no eggs or embryos, but which possessed the round body and thickened hind tibiae covered with many sensoria of the typical oviparae, were included in this group.

Experimental Method.

The method used in the various experiments followed the same general plan. A number of bean plants were inoculated with adult apterous virginoparae taken from the standard culture (= grandparent Aphids); half of these were placed in a lightproof cage receiving a photoperiod of 8 hr./24 hr. and half in a cage receiving a photoperiod of 16 hr./24 hr. and both these cages were kept at one of the six controlled temperatures used. These grandparents were left to reproduce for one to three days, after which time they were removed from the plants and the offspring they had produced left behind. The offspring (some of which were to become parents) were left in the cages in which they had been born until they reached their last (imaginal) moult (*i.e.*, throughout their nymphal period). At the end of this period a number of them were taken from each of the two cultures, and placed on new bean plants and returned to the experimental cages so that half the Aphids which had received a photoperiod of 8 hr./24 hr. during their nymphal period continued to receive this photoperiod during their adult period, while half received a photoperiod of 16 hr./24 hr. Similarly with those which had received a photoperiod of 16 hr./24 hr. during their nymphal period, half continued to receive this photoperiod during their adult period and half received a photoperiod of 8 hr./24 hr. Therefore at each of the different temperatures four groups of parent Aphids were obtained which had received different treatments of photoperiod:—

Photoperiod during nymphal period	Photoperiod during adult period*	Treatment subsequently referred to as :—
8 hr./24 hr.	8 hr./24 hr.	8 : 8
8 hr./24 hr.	16 hr./24 hr.	8 : 16
16 hr./24 hr.	8 hr./24 hr.	16 : 8
16 hr./24 hr.	16 hr./24 hr.	16 : 16

* The adult period is the period from the last (imaginal) moult until the death of the parent.

In most of the experiments each treatment was set up in duplicate (*i.e.*, two separate groups of parents), and throughout the reproductive period each group was kept distinct. At intervals of approximately two to four days, the parent Aphids were transferred to new bean shoots and returned to their respective cages, while the offspring they had produced during this period were left on the old bean plant and received a constant temperature of 19–20°C. and a photoperiod of 24 hours, until they became mature. When mature, they were collected and examined microscopically to determine their form. In this manner a succession of offspring were obtained from each group of parents throughout their adult period.

Using the method described and exposing the parents to the two photoperiods, six experiments were carried out, at temperatures of 29–30°C., 25–26°C., 19–20°C., 11–13°C., 7–11°C., and 5–9°C., respectively. A seventh experiment consisted of observation of the offspring produced by individual parent Aphids which had received the photoperiod treatments of 8:8 and 8:16 at a temperature of 19–20°C.

These gave a total of 24 different treatments of temperature and photoperiod, further details of which are given in Table I.

Control experiments.

To test the uniformity of the reaction of the standard Aphids to photoperiod and temperature throughout the series of experiments, two control experiments were carried out where the Aphids received a photoperiod treatment of 8 hr./24 hr. during their nymphal and adult periods (*i.e.*, treatment 8:8), at a temperature of 19–20°C. These conditions were arbitrarily chosen as those which caused the production of males, oviparae and apterous virginoparae bearing sensoria and the conditions used in treatment 8:8 of experiments 3 and 7, being the same, these therefore also acted as control experiments. One experiment, Control a, was carried out in the middle of the series (31.10.52–3.12.52), the other, Control b, at the end of the series (17.1.53–25.2.53).

RESULTS.

Standard Aphids.

The Aphids which were reared for many generations under the standard conditions of temperature (20°C.) and photoperiod (24 hr./24 hr.) produced apterous virginoparae almost exclusively. Alate virginoparae were encountered only infrequently, and sexual forms not at all.

Offspring of the Experimental Aphids.

(a) *Parthenogenetic offspring.*

Apterous virginoparous offspring were produced in varying proportions by all the experimental Aphids. At the higher temperatures (29–30°C., 25–26°C.) all

TABLE I.

Summary of experiments carried out.

Expt.	Temp. in °C.	Length of time in days, standard grandparents left to reproduce	Length of nymphal period, in days, of parent Aphids	Light treatments	No. parent Aphids per group	No. Aphid groups per treatment	Date of experiment from birth to death of parent Aphids
1 (Table II)	29–30	2	6 to 7	8 : 8, 8 : 16, 16 : 8	10	2 (except 16 : 16)	21.11.52–9.12.52
2 (Table III)	25–26	2	4 to 5	,,	10	2	17. 1.53–16. 2.53
3 (Fig. 1)	19–20	1	8 to 9	,,	9	2	19. 3.52–28. 4.52
4 (Fig. 2)	11–13	3	22 to 25 in 8-hour cage 21 to 24 in 16-hour cage	8 : 8, 8 : 16, 16 : 8, 16 : 16	10	2	31.10.52–29.12.52
5 (Fig. 3)	7–11	2	24 to 26 in 8-hour cage 20 to 24 in 16-hour cage	,,	11	1	22. 6.52–9. 9.52
6 (Fig. 4)	5– 9	3	39 to 42 in 8-hour cage 37 to 40 in 16-hour cage	,,	7	2	17. 1.53–7. 4.53
7 (Table IV)	19–20	1	8 to 9	8 : 8, 8 : 16	1	4	3. 6.52–24. 7.52
Control a (Table V)	19–20	2	8 to 9	8 : 8	8	2	31.10.52–3.12.52
Control b (Table V)	19–20	2	8 to 9	8 : 8	8	2	17. 1.53–25. 2.53

TABLE II.

Expt. 1 at 29–30°C.

A. Parents, 8 hr. nymphal photoperiod.

1. Parents 8 hr./24 hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al ♀	♂	♀
1– 3	20	23	24	0	0	0
3– 5	20	30	76	0	0	0
5– 7	20	9	81	0	0	0
7– 9	19	10	36	0	0	0
9–11	18	14	12	0	0	0
11–12	17	0	7	0	0	0
12–14	13	1	0	0	0	0
14–16	9	0	1	0	0	0
Totals ..	.. ..	87	237	0	0	0
Percentage of grand total ..		26·9	73·1	0	0	0

Av. no. offspring per parent=16·2

2. Parents 16 hr./24 hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap ♀ +S	Ap♀	Al♀	♂	♀
1– 3	20	19	8	0	0	0
3– 5	20	27	18	0	0	0
5– 7	19	0	0	0	0	0
7– 9	19	0	1	0	0	0
9–11	19	0	0	0	0	0
11–12	18	0	0	0	0	0
12–14	13	0	0	0	0	0
14–16	2	0	0	0	0	0
Totals ..	.. ..	46	27	0	0	0
Percentage of grand total ..		63	37	0	0	0

Av. no. offspring per parent=3·7

TABLE II—*continued*.

B. Parents, 16 hr. nymphal photoperiod.

3. Parents 8 hr./24 hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 3	20	0	0	0	0	0
3– 5	20	5	9	0	0	0
5– 7	19	1	5	0	0	0
7– 9	19	0	0	0	0	0
9–11	19	0	1	0	0	0
11–12	18	1	0	0	0	0
12–14	16	0	0	0	0	0
14–16	15	0	0	0	0	0
Totals ..	.. ..	7	15	0	0	0
Percentage of grand total		31·8	68·2	0	0	0

Av. no. offspring per parent=1·1

4. Parents 16 hr./24 hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 3	10	0	0	0	0	0
3– 5	10	0	0	0	0	0
5– 7	10	0	0	0	0	0
7– 9	10	0	0	0	0	0
9–11	8	0	0	0	0	0
11–12	8	0	0	0	0	0
12–14	6	0	0	0	0	0
14–16	0	0	0	0	0	0
Totals ..	.. ..	0	0	0	0	0

Av. no. offspring per parent=0

Ap♀ = Apterous parthenogenetic female.
Ap♀+ S = ,, ,, ,, bearing sensoria on the hind tibiae.
Al♀ = Alate ,, ,,
♀ = Oviparous female. ♂ = male.

TABLE III.

Expt. 2 at 25–26°C.

A. Parents, 8 hr. nymphal photoperiod.

1. Parents 8 hr./24 hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 4	20	26	348	0	0	0
4– 6	20	12	253	0	0	0
6– 8	20	3	277	1	0	0
8–11	19	32	142	0	0	0
11–14	19	54	73	0	0	0
14–16	19	2	40	0	0	0
16–18	19	3	8	0	0	0
18–20	17	0	4	0	0	0
20–22	12	0	0	0	0	0
22–25	6					
25–28	1					
Totals		132	1,145	1	0	0
Percentage of grand total		10·3	89·6	0·1	0	0

Av. no. offspring per parent=63·9

2. Parents 16 hr./24hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 4	20	8	361	0	0	0
4– 6	20	1	290	0	0	0
6– 8	20	17	241	0	0	0
8–11	19	4	230	0	0	0
11–14	19	2	120	0	0	0
14–16	19	3	43	0	0	0
16–18	19	2	24	0	0	0
18–20	18	0	5	0	0	0
20–22	17	0	0	0	0	0
22–25	10					
25–28	5					
Totals		37	1,314	0	0	0
Percentage of grand total		2·7	97·3	0	0	0

Av. no. offspring per parent=67·6

TABLE III—*continued*.

B. Parents, 16 hr. nymphal photoperiod.

3. Parents 8 hr./24 hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 4	20	72	296	0	0	0
4– 6	20	21	282	0	0	0
6– 8	20	3	242	0	0	0
8–11	19	27	244	0	0	0
11–14	18	42	122	0	0	0
14–16	18	11	31	0	0	0
16–18	17	2	11	0	0	0
18–20	15	0	0	0	0	0
20–22	13	0	1	0	0	0
22–25	6	0	0	0	0	0
25–28	1	0	0	0	0	0
Totals		178	1,229	0	0	0
Percentage of grand total		12·6	87·4	0	0	0

Av. no. offspring per parent=70·4

4. Parents 16 hr./24 hr. adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 4	20	27	351	0	0	0
4– 6	20	1	281	0	0	0
6– 8	20	0	267	0	0	0
8–11	19	1	192	0	0	0
11–14	19	11	146	0	0	0
14–16	18	2	32	0	0	0
16–18	17	0	3	0	0	0
18–20	17	0	3	0	0	0
20–22	15	0	0	0	0	0
22–25	7	0	0	0	0	0
25–28	1	0	0	0	0	0
Totals		42	1,275	0	0	0
Percentage of grand total		3·2	96·8	0	0	0

Av. no. offspring per parent=65·9

TABLE IV.

Expt. 7. Offspring produced by individual Aphids at 19–20°C.

A. Parents, 8 hr./24 hr. nymphal and adult photoperiod.

Aphid	1					2					3					4				
Age in days after last moult	Ap♀+S	Ap♀	Al♀	♂	♀	Ap♀+S	Ap♀	Al♀	♂	♀	Ap♀+S	Ap♀	Al♀	♂	♀	Ap♀+S	Ap♀	Al♀	♂	♀
1– 4	0	12	0	0	0	1	18	0	0	0	0	26	0	0	0	2	16	0	0	0
4– 7	0	15	0	0	0	0	14	0	0	0	0	25	0	0	0	0	15	0	0	0
7–10	0	16	0	0	0	0	16	0	0	0	0	17	0	0	0	0	12	0	0	2
10–13	0	6	0	0	2	0	1	0	6	1	0	9	0	1	1	0	1	0	0	3
13–16	0	0	0	10	1	0	4	0	11	0	0	0	0	6	0	0	0	0	12	1
16–19	0	0	0	7	0	0	0	0	3	0	0	0	0	2	0	0	0	0	2	0
19–24	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	4	0
24–28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals	0	49	0	18	3	1	53	0	21	1	0	77	0	10	1	2	44	0	18	6
Total offspring	70					76					88					70				

TABLE IV—*continued.*

B. Parents, 8 hr./24 hr. nymphal photoperiod, 16 hr./24 hr. adult period.

Aphid	5					6					7					8				
Age in days after last moult	Ap♀ +S	Ap♀	Al♀	♂	♀	Ap♀ +S	Ap♀	Al♀	♂	♀	Ap♀ +S	Ap♀	Al♀	♂	♀	Ap♀ +S	Ap♀	Al♀	♂	♀
1– 4	0	16	0	0	0	0	14	0	0	0	0	20	0	0	0	0	12	0	0	0
4– 7	0	12	0	0	0	0	14	0	0	0	0	17	0	0	0	0	13	0	0	0
7–10	0	17	0	0	0	0	14	0	0	0	0	16	0	0	0	0	10	0	0	0
10–13	0	8	0	7	0	0	7	0	0	0	0	6	0	8	0	0	3	0	2	0
13–16	0	0	0	12	0	0	1	0	7	0	0	0	0	9	0	0	0	0	11	0
16–19	0	0	0	8	0	0	0	0	6	0	0	0	0	7	0	0	0	0	9	0
19–24	0	0	0	6	0	0	0	0	1	0	0	0	0	1	0	0	0	0	6	0
24–28	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Totals	0	55	0	33	0	0	50	0	15	0	0	59	0	25	0	0	38	0	28	0
Total offspring	88					65					84					66				

	Ap♀ + S	Ap♀	Al♀	♂	♀
Percentages of forms in offspring produced by Aphids 1, 2, 3, 4 =	1	73·1	0	23·3	3·7
,, ,, ,, ,, ,, ,, ,, ,, 5, 6, 7, 8 =	0	66·7	0	33·3	0

TABLE V.

Control (a) and (b) at 19–20°C.

(*a*) Parents 8 hr./24 hr. nymphal and adult photoperiod

Age of parents in days after last moult	No. of parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 5	16	172	189	0	0	0
5– 9	16	81	205	0	0	47
9–12	(Offspring from 8 of the parents lost)					
	offspring from 5 parents	2	21	0	34	20
12–16	10	7	27	0	91	0
16–20	10	2	6	0	34	0
20–25	7	1	1	0	5	0
Totals		265	449	0	164	67
Adjusted totals (to make up for offspring lost days 9–12).. ..		268	483	0	218	99
Percentage of grand total ..		25·1	45·1	0	20·4	9·3

Av. no. offspring per parent=66·5

(*b*) Parents 8 hr./24 hr. nymphal and adult photoperiod

Age of parents in days after last moult	No. parents alive at end of period	Offspring				
		Ap♀ +S	Ap♀	Al♀	♂	♀
1– 5	15	198	172	0	0	0
5– 8	15	62	174	0	0	3
8–11	15	23	147	0	24	14
11–13	15	4	50	0	66	2
13–17	14	11	30	0	126	2
17–23	13	1	5	0	57	0
23–30	3	0	0	0	0	0
Totals		299	578	0	273	21
Percentage of grand total ..		25·5	49·4	0	23·3	1·8

Av. no. offspring per parent=78

TABLE VI.

Total numbers and percentages of the different forms of offspring produced by apterous virginoparous *A. pisum* which have received various treatments of photoperiod and temperature.

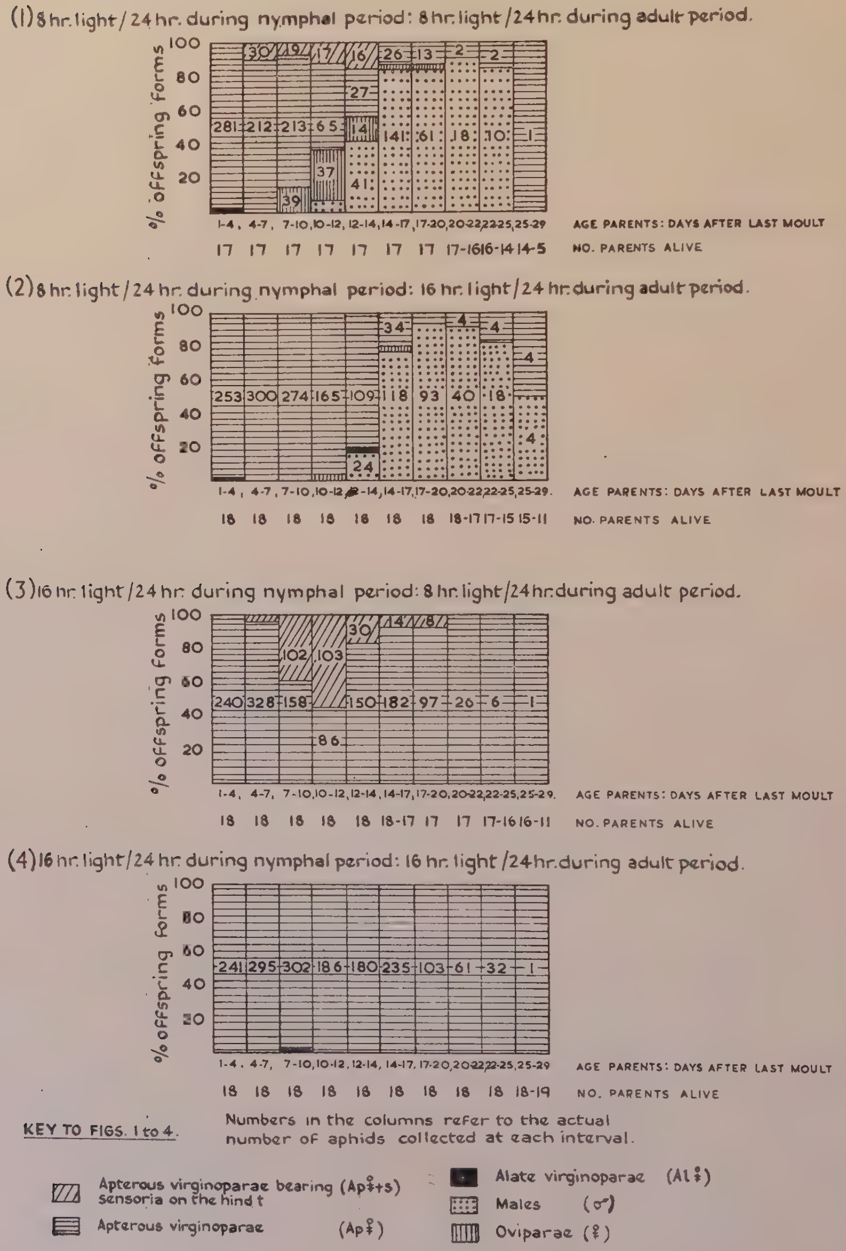
Treatment of parent Aphids				Offspring											
Expt.	Temp. in °C.	Photoperiod/24 hr.		Totals					Percentages					Grand totals	Initial no. parents
		Nymphal stage	Adult stage	Ap♀ +S	Ap♀	Al♀	♀	♂	Ap♀ +S	Ap♀	Al♀	♀	♂		
1	29–30	8 hr.	8 hr.	87	237	0	0	0	27	73	0	0	0	324	20
		8 hr.	16 hr.	46	27	0	0	0	63	37	0	0	0	73	20
		16 hr.	8 hr.	7	15	0	0	0	32	68	0	0	0	22	20
		16 hr.	16 hr.	0	0	0	0	0	0	0	0	0	0	0	10
2	25–26	8 hr.	8 hr.	132	1,145	1	0	0	10	90	0·1	0	0	1,278	20
		8 hr.	16 hr.	37	1,314	0	0	0	3	97	0	0	0	1,351	20
		16 hr.	8 hr.	178	1,229	0	0	0	13	87	0	0	0	1,407	20
		16 hr.	16 hr.	42	1,275	0	0	0	3	97	0	0	0	1,317	20
3	19–20	8 hr.	8 hr.	82	842	2	91	280	6	65	0·2	7	22	1,303	17
		8 hr.	16 hr.	1	1,155	3	2	297	0·1	79	0·2	0·1	20	1,458	18
		16 hr.	8 hr.	262	1,274	0	0	0	17	83	0	0	0	1,536	18
		16 hr.	16 hr.	0	1,535	7	0	0	0	99	1	0	0	1,542	18
4	11–13	8 hr.	8 hr.	66	41	0	592	28	9	6	0	81	4	727	20
		8 hr.	16 hr.	39	137	8	497	203	4	16	1	56	23	884	19
		16 hr.	8 hr.	416	327	0	0	0	56	40	0	0	0	743	20
		16 hr.	16 hr.	24	688	103	0	0	3	84	13	0	0	815	20
5	7–11	8 hr.	8 hr.	151	129	0	59	0	44	38	0	17	0	339	11
		8 hr.	16 hr.	18	299	88	53	0	4	65	19	12	0	458	11
		16 hr.	8 hr.	292	197	15	0	0	57	39	3	3	0	504	11
		16 hr.	16 hr.	2	300	268	0	0	0·3	53	47	0	0	570	11
6	5–9	8 hr.	8 hr.	213	43	0	35	0	73	15	0	12	0	291	14
		8 hr.	16 hr.	57	251	2	56	0	16	69	1	15	0	366	14
		16 hr.	8 hr.	269	135	0	0	0	67	33	0	0	0	404	14
		16 hr.	16 hr.	40	507	21	0	0	7	89	4	0	0	568	14
7	19–20	8 hr.	8 hr.	3	223	0	11	67	1	73	0	4	23	301	4
		8 hr.	16 hr.	0	202	0	0	101	0	67	0	0	33	303	4
Control a	19–20	8 hr.	8 hr.	268	483	0	99	218	25	45	0	9	20	1,068	16
Control b	19–20	8 hr.	8 hr.	299	578	0	21	273	25	49	0	2	23	1,171	15

Figs. 1–4.—Results of experiments 3–6 showing the percentage of the various forms of offspring produced, at successive intervals throughout reproduction, by apterous virginoparous *A. pisum*, which received four treatments of photoperiod at temperatures of 19–20°C., 11–13°C., 7–11°C. and 5–9°C.

Fig. 1.

TEMP. 19 – 20°C.

PHOTOPERIOD TREATMENT OF PARENT APTERAE:-



(1) 8 hr. light/24 hr. during nymphal period: 8 hr. light/24 hr. during adult period.

(2) 8 hr. light/24 hr. during nymphal period: 16 hr. light/24 hr. during adult period.

(3) 16 hr. light/24 hr. during nymphal period: 8 hr. light/24 hr. during adult period.

(4) 16 hr. light/24 hr. during nymphal period: 16 hr. light/24 hr. during adult period.

KEY TO FIGS. 1 to 4.

Numbers in the columns refer to the actual number of aphids collected at each interval.

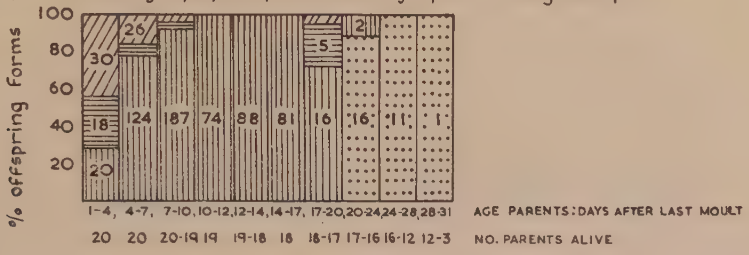
% offspring forms
100
80
60
40
20
30
19
17
16
26
13
2
2
27
281
212
213
65
4
141
61
18
10
1
37
41
39
1-4, 4-7, 7-10, 10-12, 12-14, 14-17, 17-20, 20-22, 22-25, 25-29
AGE PARENTS: DAYS AFTER LAST MOULT
17 17 17 17 17 17 17 17-16 16-14 14-5
NO. PARENTS ALIVE
34
4
4
4
253
300
274
165
109
118
93
40
18
4
24
18 18 18 18 18 18 18 18-17 17-15 15-11
102
103
30
14
8
240
328
158
150
182
97
26
6
1
86
18 18 18 18 18 18-17 17 17 17-16 16-11
241
295
302
186
180
235
103
61
32
1
18 18 18 18 18 18 18 18 18 18-19
▨ Apterous virginoparae bearing (Ap♀+s) sensoria on the hind t
▤ Apterous virginoparae (Ap♀)
■ Alate virginoparae (Al♀)
⠿ Males (♂)
▥ Oviparae (♀)

Fig. 2.

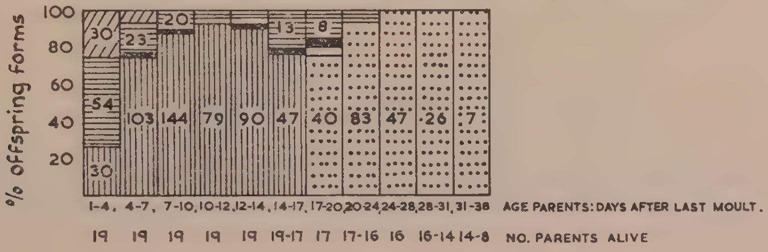
TEMP. 11-13 °C.

PHOTOPERIOD TREATMENT OF PARENT APTERAE:-

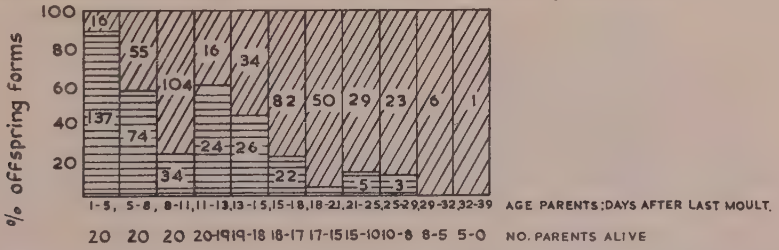
(1) 8 hr. light/24 hr. during nymphal period: 8 hr. light/24 hr. during adult period



(2) 8 hr. light/24 hr. during nymphal period: 16 hr. light/24 hr. during adult period



(3) 16 hr. light/24 hr. during nymphal period: 8 hr. light/24 hr. during adult period



(4) 16 hr. light/24 hr. during nymphal period: 16 hr. light/24 hr. during adult period

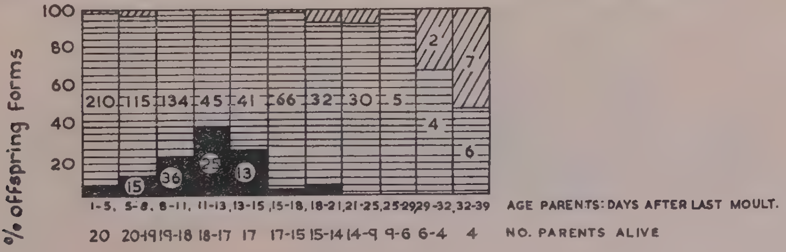
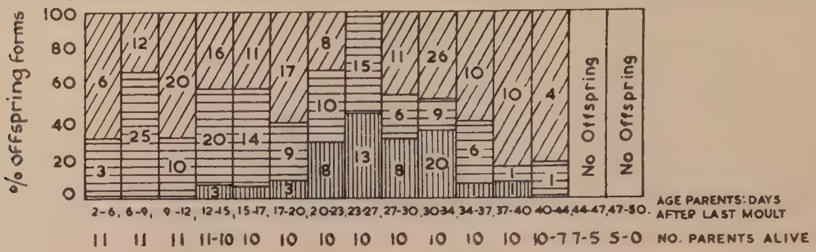


Fig. 3

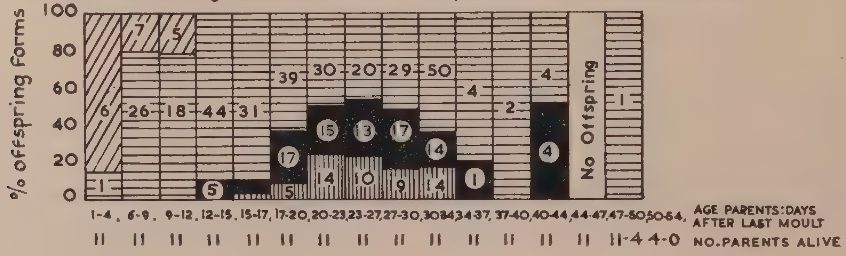
TEMP. 7-11°C.

PHOTOPERIOD TREATMENT OF PARENT APTERAE:-

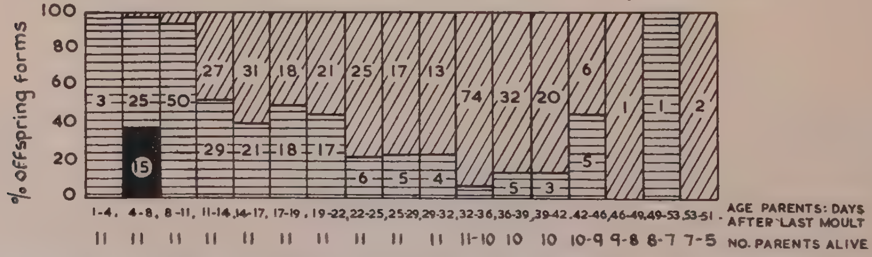
(1) 8 hr. light / 24 hr. during nymphal period: 8 hr. light / 24 hr. during adult period.



(2) 8 hr. light / 24 hr. during nymphal period: 16 hr. light / 24 hr. during adult period.



(3) 16 hr. light / 24 hr. during nymphal period: 8 hr. light / 24 hr. during adult period.



(4) 16 hr. light / 24 hr. during nymphal period: 16 hr. light / 24 hr. during adult period.

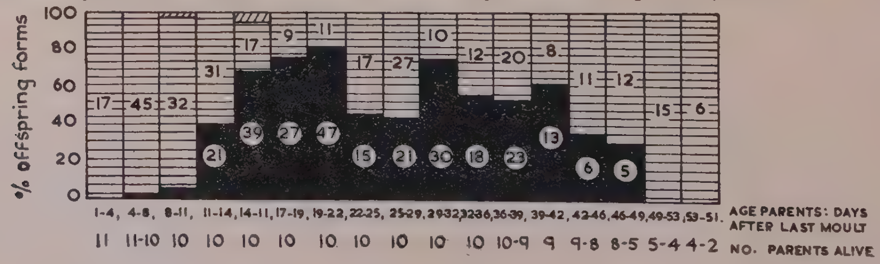
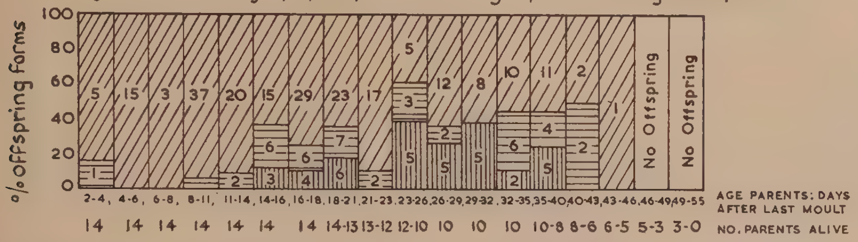


Fig. 4.

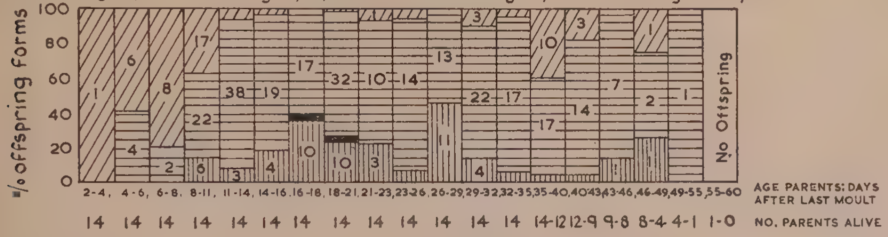
TEMP. 5-9°C.

PHOTOPERIOD TREATMENT OF PARENT APTERAE:-

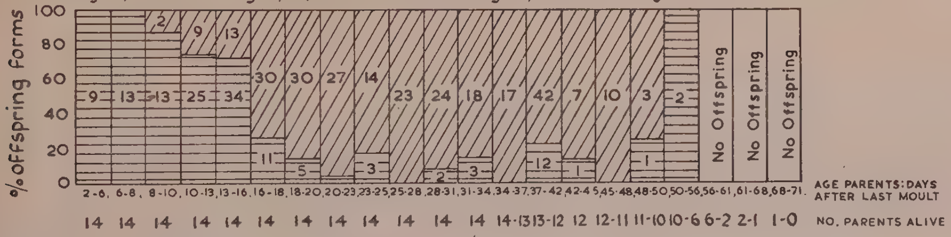
(1) 8 hr. light/24 hr. during nymphal period: 8 hr. light/24 hr. during adult period



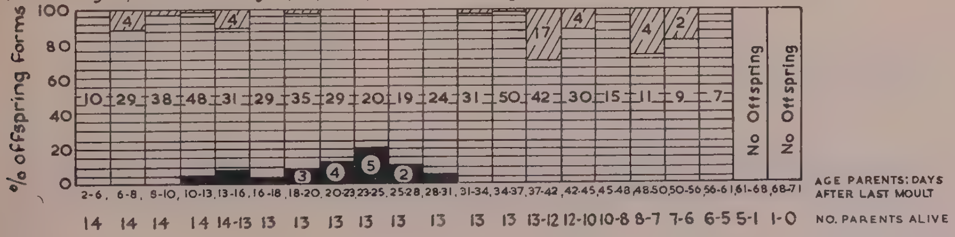
(2) 8 hr. light/24 hr. during nymphal period: 16 hr. light/24 hr. during adult period.



(3) 16 hr. light/24 hr. during nymphal period: 8 hr. light/24 hr. during adult period.



(4) 16 hr. light/24 hr. during nymphal period: 16 hr. light/24 hr. during adult period.



the offspring were of this type (with normal or abnormal hind tibiae) irrespective of photoperiod exposure of the parent (Tables II & III). At the other temperatures this form was produced almost exclusively by Aphids which received a daily photoperiod of 16 hr. during the nymphal period (*i.e.*, treatments 16:8 and 16:16), (figs. 1–4), except in those treatments which favoured the production of a high proportion of alatae (*i.e.*, treatments 16:16, at 11–13°C. and 7–11°C.).

Apterous virginoparous offspring bearing sensoria on the hind tibiae were produced by the parents under most of the different experimental conditions used. The proportion of this form, however, varied considerably with the treatments. In general, at any one temperature the largest proportion was produced by those parents which received a daily photoperiod of 8 hr. during the adult period (*i.e.*, treatments 16:8 and 8:8) (Table VI); this was particularly noticeable at the lower temperatures (11–13°C., 7–11°C. and 5–9°C.) where the greatest proportions (44–73%) of this form were produced (figs. 2, 3 & 4). At 29–30°C. an unusually high proportion of this form was produced with a photoperiod of 8:16. At this temperature, however, comparatively few offspring were produced (Table II) and reproduction was mainly confined to a short period following the maturation of the parent. It is worth pointing out, moreover, that if reproduction had been similarly restricted to a few days following maturity in the Aphids kept at the

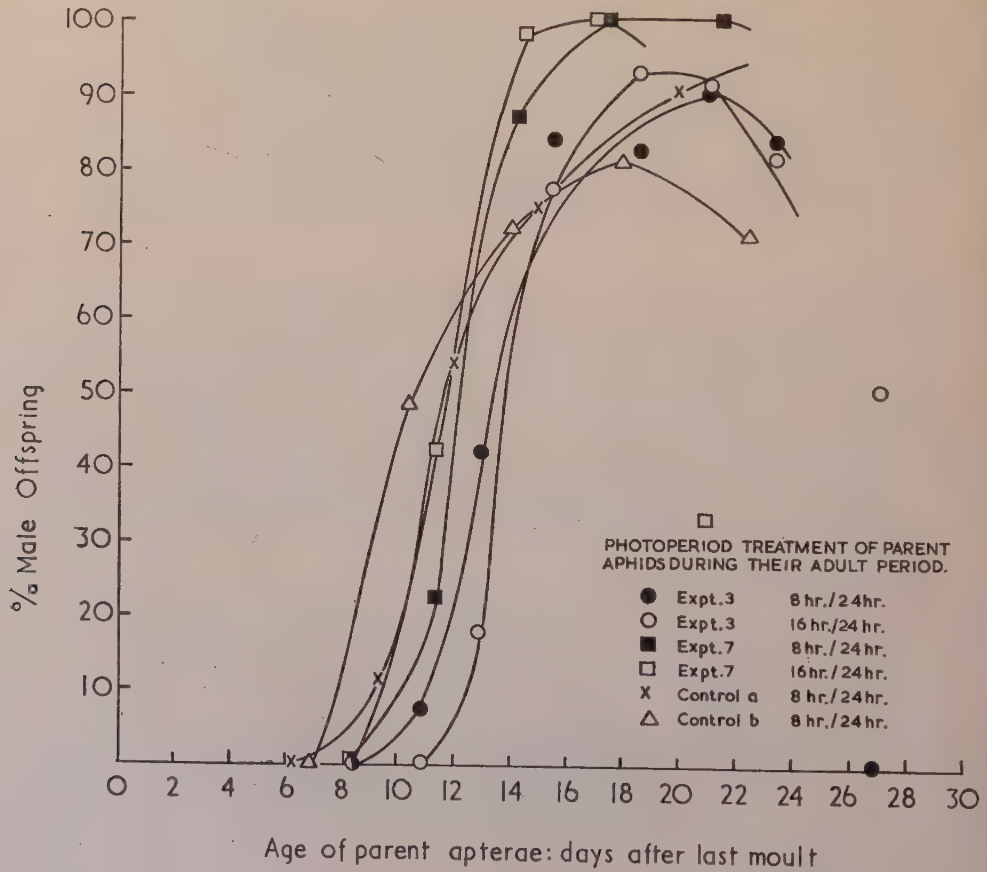


Fig. 5.—Proportion of male offspring produced at successive intervals throughout reproduction by apterous virginoparous *A. pisum* which had received a photoperiod of 8 hr./24 hr. during their nymphal period and a temperature of 19–20°C.

other temperatures, which received an 8:16 photoperiod, a similar result would have been obtained, since they also produced a high proportion of this form during the period immediately following maturity (figs. 2, 3 & 4).

Alate virginoparous offspring were not produced in 14 of the 24 different experimental treatments used. At temperatures above 19°C. they were produced very infrequently ($< 1\%$), while at lower temperatures the largest proportions were produced by those parents which received a photoperiod of 16 hr. during the adult period (1–47%). The most favourable conditions appeared to be a low temperature (7–11°C.) and a photoperiod of 16 hr. during both the nymphal and adult period (Expt. 5) where 47 per cent. of the total offspring were winged virginoparae (fig. 3).

(b) *Sexual forms.*

Sexual forms were produced *only* by Aphids which had received a photoperiod of 8 hr./24 hr. *during the nymphal period.* At the higher temperatures (25–26°C. and 29–30°C.) no sexual forms were produced even with an 8 hr. photoperiod.

Males were only produced at temperatures of 19–20°C. and 11–13°C. (figs. 1 & 2). The results of four separate experiments at 19–20°C. (Expts. 3, 7, controls a and b) showed that males did not appear among the offspring until approximately 8 to 13 days of the adult period had elapsed. The proportion of male offspring then increased as reproduction continued and reached a maximum of 80–100 per cent. after 17 to 20 days from the time that reproduction commenced (fig. 5). Variation in the photoperiod treatment of the parent Aphid during the adult period did not appear to affect either the proportion of male offspring produced or the time at which they appeared.

Oviparous offspring were produced only at the four lower temperatures (Table VI). The most favourable temperature was 11–13°C. where 56–81 per cent. of the total offspring were of this form. Except for the experiment at 5–9°C., a photoperiod treatment of 8 hr./24 hr. during the adult period appeared to give a higher proportion of oviparous offspring than a photoperiod of 16 hr./24 hr. (figs. 1, 2, 3 & 4). Table VII shows the variation in form of the oviparous offspring produced by the parents kept at the three lower temperatures.

Forms produced by individual apterae.

From Expt. 7, where the offspring produced by individual Aphids were kept separate, it was found that a single parent, given a suitable temperature and photoperiod, could produce during its lifetime apterous virginoparae (with and without sensoria on the hind tibiae), males and oviparae (Table IV).

The effect of temperature and photoperiod on longevity and reproduction.

Approximate data can be obtained from these experiments showing the influence of photoperiod and temperature on the longevity and reproduction of apterous virginoparous forms of *A. pisum.*

The length of nymphal period at temperatures of 26°C. and below increased with decrease in temperature, lasting approximately four to five days at 25–26°C. and 37 to 42 days at 5–9°C. At temperatures below 11°C., parent-nymphs receiving a photoperiod of 8 hr. appeared to take one to two days longer to develop than those receiving a photoperiod of 16 hr. (Table I).

The length of adult period also increased with decrease in temperature. At 30°C. most of the Aphids died 16 days after their last (imaginal) moult and at 5–9°C. 71 days after their last (imaginal) moult (Tables II, III & IV; figs. 1, 2, 3 & 4).

The total number of offspring was greatest at 19–20°C., at which temperature from 77 to 86 offspring per parent were produced according to the photoperiod treatment of the parents. The smallest number of offspring was obtained at

TABLE VII.

Variation in the form of the oviparous offspring produced by parents kept at lower temperatures.

Expt.	Photoperiod treatment of parent	Offspring					
		(1) Eggs+embryos		(2) No eggs	(3) Eggs only		
		0 to few S*	Many S	Many S	O to few S (up to approx. 20)	Moderate no. S	Many S
4 (11–13°C.)	8:8	1	3	89	0	0	490
	8:16	4	0	417	5	0	75
5 (7–11°C.)	8:8	1	3	11	2	0	39
	8:16	1	0	20	10	0	20
6 (5–9°C.)	8:8	0	3	9	0	2	22
	8:16	0	3	17	0	0	36

* S = Sensoria on the hind tibiae.

29–30°C. and 5–9°C., where between 0 to 16 and 20 to 34 offspring per parent were produced, respectively, according to the photoperiod treatment of the parents (fig. 6).

Abnormal effects of high temperatures.

Offspring produced by those Aphids which received a temperature treatment of 29–30°C. showed several abnormalities, namely, small size when mature, paucity or lack of embryos and variable period required to reach maturity.

The most obvious difference between the offspring obtained at the highest temperature and those obtained at the other temperatures was their size when mature. Measurement of 64 of the offspring produced at 29–30°C., chosen at random, showed that their length (measured from the base of the cauda to the base of the antennae) varied between 1·7 and 2·9 mm. with an average length of 2·2 mm. Similar measurements with standard individuals gave the following results: 27 standard Aphids varied in length from 3·1 to 4·2 mm., average length 3·8 mm. (Pl. XIX, figs. 4 a & b). The parent Aphids (which were kept at the high temperature from birth till death) showed, however, no such abnormality of size; 10 Aphids were measured from each of the parent cultures—*i.e.*, those receiving an 8 hr. and those a 16 hr. daily photoperiod during their nymphal period—and found to vary in length from 3·3 to 3·6 mm., average 3·5 mm., and from 3·4 to 3·6 mm., average 3·4 mm., respectively.

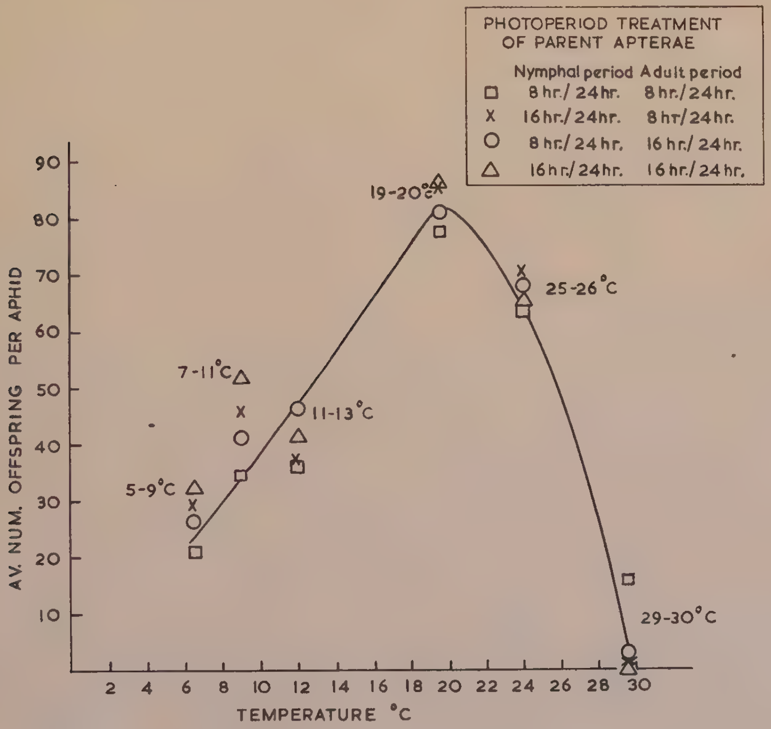


Fig. 6.—Effect of temperature and photoperiod on the average number of offspring produced per apterous virginoparous *A. pisum*.

In contrast to the offspring obtained at the other temperatures which had many embryos within their bodies at maturity, the offspring obtained at 29–30°C.

had few or none. Furthermore, whereas the offspring obtained at temperatures lower than 29–30°C. took eight to nine days to reach maturity when they were transferred to 20°C., those produced at 29–30°C. frequently took longer, a period as long as 15 days being required in some cases.

Discussion.

The results of the present work suggest that *A. pisum* is influenced by photoperiod and temperature in a manner similar to that found with the other species of Aphids which have been studied (Marcovitch, 1924; Davidson, 1929; de Fluiter, 1950; Wilson, 1938; Bonnemaison, 1951), in that a long photoperiod and a high temperature favour the production of parthenogenetic forms and a short photoperiod and low temperatures (20°C. and below) favour the production of sexual forms.

The results also suggest that the optimum temperature for the production of males is higher than the optimum temperature for the production of oviparae. This behaviour of *A. pisum* therefore resembles that of *Brevicoryne brassicae* (L.) and *Myzus persicae* (Sulz.), since the experiments of Bonnemaison (1951) with these two species showed that males could be produced at higher temperatures than oviparae. In the present work it was further shown that under the conditions used, male offspring were produced over a more limited range of temperature than were oviparous offspring. In this connexion it is of interest that Wilson (1938), on the basis of his results with *Aphis chloris* Koch, suggested that the conditions favouring the production of males lie within "narrow environmental boundaries" and that he found with *A. chloris* that, although oviparae were produced under a wide variety of conditions, males were produced only rarely and in small numbers.

It must be borne in mind, however, that the experiments described here were of a limited nature and consequently comparison with the work of other authors is difficult, and the present results can only indicate and not define the conditions which favour or inhibit the production of the various forms of *A. pisum*. These limitations are twofold; in the first place only the offspring produced by apterae have been studied and, secondly, the Aphids were exposed to the various experimental conditions for approximately one generation only. This latter limitation is important because the work of other authors (*e.g.*, Bonnemaison, 1951; Wilson, 1938) suggests that the proportion of the various forms of offspring produced after exposure to certain conditions for one generation may differ from those produced after exposure to these conditions for several generations. However, in the present experiments it is thought that those treatments which induced sexual forms would also have induced sexual forms in successive generations had reproduction been allowed to continue; it is possible, on the other hand, that some of those treatments which favoured the production of parthenogenetic forms alone would not have continued to favour this form exclusively with successive generations. In the former instance, a change in conditions induced a change in the form of offspring from exclusively parthenogenetic to parthenogenetic plus sexual, while in the latter instance no change was brought about.

The results of the present work show that by controlling the conditions to which an apterous parthenogenetic parent of *A. pisum* is exposed during the period from just before birth until the last (imaginal) moult (the nymphal period), it is possible to bring about, or prevent, the production of sexual forms among the offspring, while it was not found possible to cause or prevent production of sexual forms by controlling the treatments received by the parent Aphids subsequent to the last (imaginal) moult (*i.e.*, during the adult period). However, it is worth pointing out that certain experiments suggested that the treatment received during the reproductive period may have influenced the number of oviparae produced. The results as a whole indicate that by the time an aptera reaches maturity the fates of the enclosed embryos (*i.e.*, whether to be sexual or parthenogenetic) are determined, and that for the most part such determination takes place during the nymphal period of the parent. It is of course possible that the fate of some of the embryos is determined before the birth of the parent Aphid, a fact which would not have been brought out in the present experiments. Apparently, however, not all species of Aphids behave in this manner. The results of Wilson (1938), de Fluiter (1950) and Shull (1930*b*) showed that with some species it is possible to induce or prevent the appearance of sexual forms (oviparae) by treatment of the parent during the adult period, and it is of course possible that a similar effect might have been obtained with *A. pisum* if appropriate experimental conditions had been used. On the other hand, it may be that in the case of *A. pisum* either the embryos develop more rapidly than in these other species and hence all of the embryos have passed beyond the point at which they are capable of determination by the time the parent is mature, or that the point at which determination takes place occurs at an earlier stage in the development of *A. pisum* than in the other species studied.

Aphids intermediate between the parthenogenetic and oviparous form were obtained after some of the experimental treatments. These were not studied in detail, but the number of apterous virginoparous offspring bearing sensoria on the hind tibiae were counted and the results indicate that the photoperiod the Aphids received either prior to or just after birth had the greatest influence on the production of this intermediate form. It seems therefore that the determination of the character of the hind tibiae occurs late in development. In this respect *A. pisum* is similar to *Macrosiphum euphorbiae* (Thos.) (Shull, 1930*b*, as *solanifolii* (Ashm.)).

The results of the present work suggest that the production of winged virginoparae in *A. pisum* can be influenced by temperature and photoperiod, a low temperature and long photoperiod (16 hr.) given during the adult stage of the parent Aphid favouring the appearance of winged parthenogenetic forms amongst the offspring. Essentially similar results were obtained with *Macrosiphoniella sanborni* (Gill.) by White (1946) (as *Macrosiphum*), but Shull (1932) using *M. euphorbiae* did not find a systematic response to photoperiod. For example, while in one set of experiments he found that a photoperiod of 8 hr. was most effective for the production of winged offspring, in other experiments using five separate clones, some clones produced most winged offspring when given continuous light while others did so when given an alternation of light and darkness.

Shull (1930*a*) obtained evidence that with *M. euphorbiae* the external stimuli of temperature and light affect wing determination before birth. With *M. sanborni* also, it appears that wing determination occurs before birth, since Kitzmiller (1950) has demonstrated that the wings are already differentiated in the embryo. The present results show that wing formation in *A. pisum* can be affected by the photoperiod (at certain temperatures) acting on a developing Aphid at a stage either while it is within the adult parent or shortly after its birth (*i.e.*, during the adult period of the parent Aphid). This result suggests therefore that in *A. pisum* wing determination occurs either shortly before or after birth. However, although it seems that the stimuli given late in the development of an Aphid actually determine wing formation, the present experiments also suggest that the stimuli an Aphid receives while it is developing within the nymphal parent can also have some influence on wing production. For example, it was found that those parent Aphids kept at 7–11°C. which received a photoperiod of 16 hr. during both the nymphal and adult periods produced more winged offspring than those which received this photoperiod during the adult period only. Although overcrowding and starvation have been shown most frequently to stimulate wing production in Aphids (Gregory, 1917; Wadley, 1923; Reinhard, 1927; Davidson, 1929; Schaefer, 1938), it is unlikely that these factors affected the present results. The number of Aphids per plant was never high and was less at the lower than at the higher temperatures.

It was found that *A. pisum* produced the largest number of offspring at 20°C., while at temperatures below 20°C. there was a decrease in reproduction with decrease in temperatures and this was accompanied by an increase in the length of life. A similar relationship was observed with *M. persicae*, by Fenjves (1945). Temperatures of 29–30°C. were found to be harmful to *A. pisum* although the harmful effects were not apparent until the second generation. Lawson (1941) mentions that high temperatures cause a reduction in size and lengthening of nymphal period in Aphids, and both these characteristics were observed in the present experiments when the Aphids received a temperature of 29–30°C. Ehrenhardt (1940) found that at 30°C. *Eriosoma lanigerum* (Hsm.) could develop but did not produce offspring, while Fenjves (1945) found that *M. persicae* failed to develop completely at this temperature. *A. pisum* therefore appears to be slightly more heat resistant than these species. However, it seems that there can be considerable variation within a species which has a wide geographical range, as Rattan Lal (1951) working with *M. persicae* in India, apparently got normal reproduction and development at 30°C.

Since apterous virginoparae of *A. pisum* cannot be readily distinguished by eye from oviparae, where virginoparae are required for experimental purposes (*e.g.*, for comparing the insecticidal properties of substances) it is important that oviparae should be excluded from the cultures. The present experiments show that a temperature of 20°C. and photoperiod of 16 hr./24 hr. favour the rapid production of apterous virginoparous forms almost exclusively while avoiding the production of sexual forms completely. However, to prevent the production of sexual forms it is probably sufficient to control the photoperiod only. High temperatures should be avoided since they are detrimental to reproduction.

It has been shown that a change in photoperiod, temperature, and other environmental conditions can, within a short time, affect the form of a developing Aphid and such a change must initially affect its physiology. From this point of view, it seems desirable that Aphids, which are to be used as experimental subjects in any work which may affect the physiology of the insect, should be reared under carefully controlled conditions.

Summary.

The effect of photoperiod and temperature on the production of the various forms of *Acyrthosiphon pisum* (Harris) has been studied. In this study apterous virginoparous females were exposed throughout their lifetime to two photoperiods (8 hr./24 hr. and 16 hr./24 hr.) and six different temperatures. At each of the temperatures the apterae (parent Aphids) received one of four treatments of photoperiod, *i.e.*, (1) 8 hr./24 hr. photoperiod throughout their whole life; (2) 8 hr./24 hr. photoperiod during the period from birth until the last (imaginal) moult (nymphal period), followed by 16 hr./24 hr. photoperiod from the last (imaginal) moult until death (the adult period); (3) 16 hr./24 hr. throughout life; (4) 16 hr./24 hr. during the nymphal period followed by 8 hr./24 hr. during the adult period. The offspring produced by the various parents were collected at successive intervals, and their form determined.

Four main forms of offspring were produced: apterous and alate virginoparae, males and oviparae. In addition, a subsidiary form of the apterous virginoparae was obtained, which had sensoria on the hind tibiae.

Sexual forms were produced at all the temperatures below 20°C., but only

by those parents which received a photoperiod of 8 hr./24 hr. during their nymphal period.

Parent apterae kept at temperatures of 25–26°C. and 29–30°C. that received a photoperiod of 16 hr./24 hr. during their nymphal period, produced no sexual forms.

The photoperiod received by parent Aphids during their adult period had no effect on the proportion of sexual offspring they produced.

Males were only produced at 19–20°C. and at 11–13°C.; the largest proportion was produced at 19–20°C., where between 20–30 per cent. of the total offspring were males.

Females were produced at all of the temperatures below 20°C. The highest proportion were produced at 11–13°C., where between 56 and 80 per cent. of the total were oviparae.

Alatae were rarely produced in large numbers. The largest proportions were produced at the lower temperatures by those parents which received a photoperiod of 16 hr./24 hr. throughout their nymphal and adult periods.

Apterous virginoparae bearing sensoria on the hind tibiae were produced at all temperatures, the largest proportion being produced by parents which received a photoperiod of 8 hr./24 hr. during their adult period.

Maximum reproduction occurred at 19–20°C., decreasing at higher and lower temperatures.

At high temperatures (29–30°C.) few offspring were produced. They frequently took an abnormally long time to develop, and when mature were small in size.

Length of life of the parents increased with a decrease in temperature.

Acknowledgements.

I wish to thank Dr. C. Potter for his valuable help and advice throughout the course of the investigations, and Mr. J. P. Doncaster who kindly read the manuscript and supervised the photographic work.

References.

Bonnemaison, L. (1951). Contribution à l'étude des facteurs provoquant l'apparition des formes ailées et sexuées chez les Aphidinae.—Ann. Inst. Rech. agron. Sér. C. Ann. Epiphyt., **2**, pp. 1–380.

Davidson, J. (1929). On the occurrence of the parthenogenetic and sexual forms in *Aphis rumicis* L., with special reference to the influence of environmental factors.—Ann. appl. Biol., **16**, pp. 104–134.

Ehrenhardt, H. (1940). Der Einfluss von Temperatur und Feuchtigkeit auf die Entwicklung und Vermehrung der Blutlaus.—Arb. physiol, angew. Ent., **7**, pp. 150–168.

Fenjves, P. (1945). Beiträge zur Kenntnis der Blattlaus *Myzus* (*Myzodes*) *persicae* Sulz., Überträgerin der Blattrollkrankheit der Kartoffel.—Mitt. schweiz. ent. Ges., **19**, pp. 489–611.

de Fluiter, H. J. (1950). De invloed van daglengte en temperatuur op het optreden van de geslachtsdieren bij *Aphis fabae* Scop., de zwarte bonenluis.—Tijdschr. PlZiekt., **56**, pp. 265–285.

Gregory, L. H. (1917). The effect of starvation on the wing development of *Microsiphum destructor*.—Biol. Bull., Woods Hole, **33**, pp. 296–303.

Kitzmiller, J. B. (1950). The time interval between determination and differentiation of wings, ocelli, and wing muscles in the Aphid *Macrosiphum sanborni* (Gillette).—Amer. Nat., **84**, pp. 23–50.

Lawson, C. A. (1941). The effect of temperature on longevity, reproduction and growth in Aphids.—Genetics, **26,** p. 159.

Marcovitch, S. (1923). Plant lice and light exposure.—Science, **58,** pp. 537–538.

Marcovitch, S. (1924). The migration of the Aphididae and the appearance of the sexual forms as affected by the relative length of daily light exposure.—J. agric. Res., **27,** pp. 513–522.

Rattan Lal, R. (1951). Biology and control of *Myzus persicae* Sulzer as a pest of potato at Delhi.—Indian J. agric. Sci., **20,** pp. 87–100.

Reinhard, H. J. (1927). The influence of parentage, nutrition, temperature, and crowding on wing production in *Aphis gossypii,* Glover.—Bull. Tex. agric. Exp. Sta., no. 353, 19 pp.

Rivnay, E. (1937). Moisture as the factor affecting wing development in the Citrus Aphis, *Toxoptera aurantii,* Boy.—Bull. ent. Res., **28,** pp. 173–179.

Schaefer, C. W. (1938). Physiological conditions which produce wing development in the Pea Aphid.—J. agric. Res., **57,** pp. 825–841.

Shull, A. F. (1929). The effect of intensity and duration of light and of duration of darkness, partly modified by temperature, upon wing-production in Aphids.—Arch. EntwMech. Org., **115,** pp. 825–851.

Shull, A. F. (1930*a*). Control of gamic and parthenogenetic reproduction in winged Aphids by temperature and light.—Z. indukt. Abstamm.- u. VererbLehre, **55,** pp. 108–126.

Shull, A. F. (1930*b*). Order of embryonic determination of the differential features of gamic and parthenogenetic Aphids.—Z. indukt. Abstamm.- u. VererbLehre, **57,** pp. 92–111.

Shull, A. F. (1932). Clonal differences and clonal changes in the Aphid *Macrosiphum solanifolii.*—Amer. Nat., **66,** pp. 385–419.

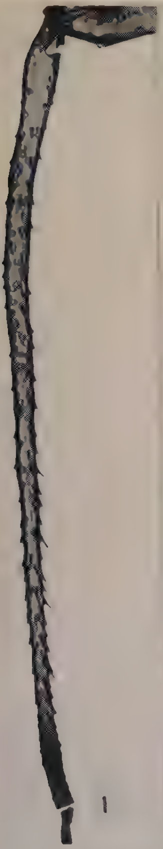
Shull, A. F. (1942). The mechanism through which light and heat influence genetic factors for wing development in Aphids.—J. exp. Zool., **89,** pp. 183–195.

Smith, L. M. (1937). Growth, reproduction, feeding, and wing development of the Mealy Plum Aphid in relation to climatic factors.—J. agric. Res., **54,** pp. 345–364.

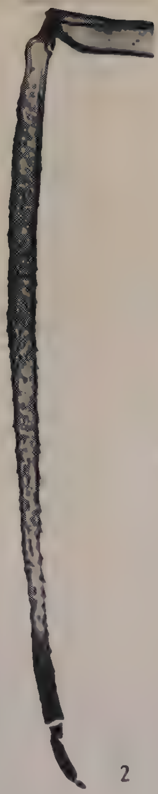
Wadley, F. M. (1923). Factors affecting the proportion of alate and apterous forms of Aphids.—Ann. ent. Soc. Amer., **16,** pp. 279–303.

White, W. S. (1946). The environmental conditions affecting the genetic mechanism of wing production in the Chrysanthemum Aphid.—Amer. Nat., **80,** pp. 245–270.

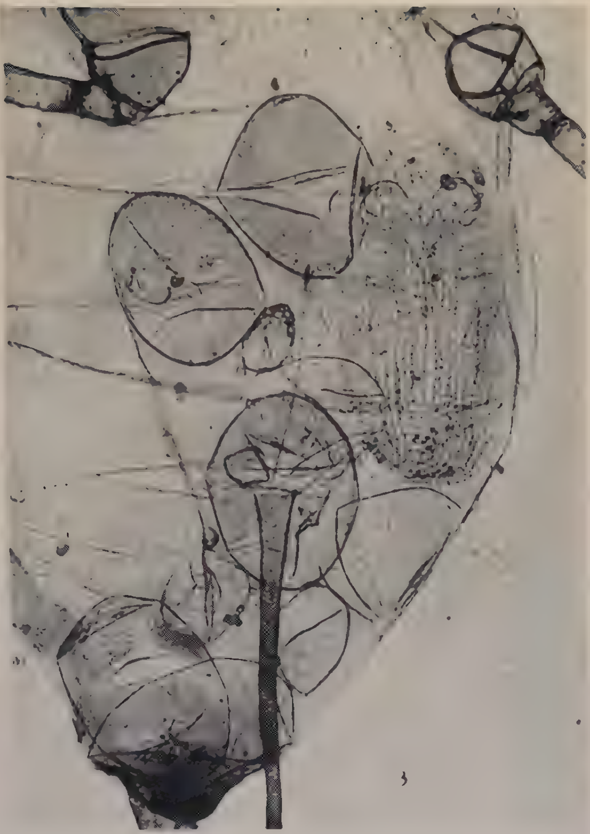
Wilson, F. (1938). Some experiments on the influence of environment upon the forms of *Aphis chloris* Koch (Aphididae).—Trans. R. ent. Soc. Lond., **87,** pp. 165–180.



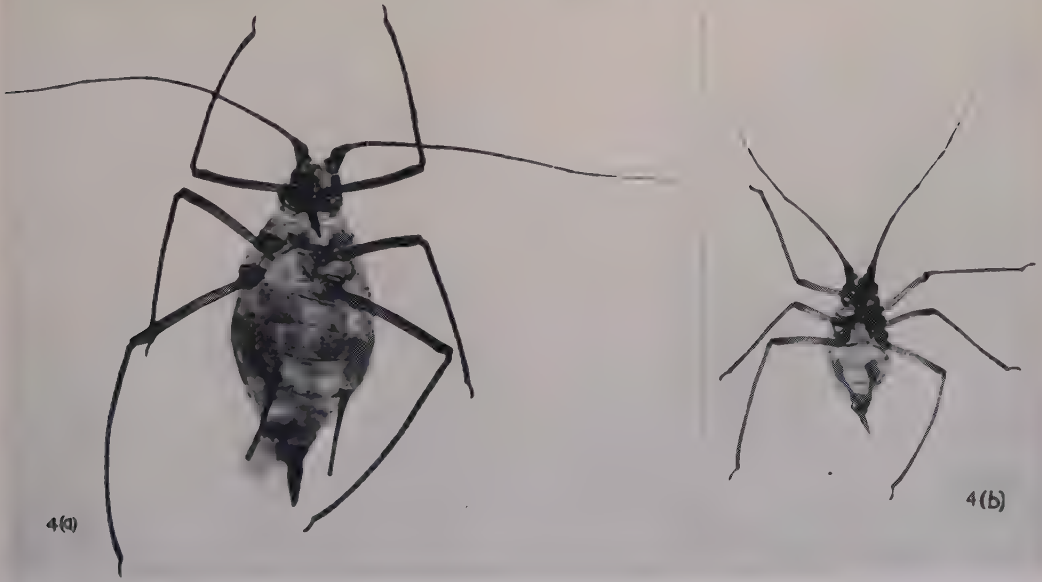
1



2



3



4(a)

4(b)

FIG. 1. *A. pisum.* Hind tibia of an apterous virginopara bearing a moderate number of sensoria. (×38.)

FIG. 2. *A. pisum.* Hind tibia of an ovipara. (×45.)

FIG. 3. *A. pisum.* Ovipara containing embryo and eggs. (×45.)

FIG. 4. *A. pisum.* Typical mature apterous virginoparæ, (a) and (b), the offspring of parents reared at 20° C. and 30° C., respectively. (×10.)

INSECTICIDAL DUSTS FOR THE PROTECTION OF STORED PEAS AND BEANS AGAINST BRUCHID INFESTATION.

E.H.N.

By E. A. Parkin and G. T. Bills
Department of Scientific and Industrial Research, Pest Infestation Laboratory, Slough, Bucks.

Introduction.

Pulses, including peas, cowpeas and beans, are very valuable crops and are grown in great variety in most parts of the world. The roots increase the soil nitrogen and the haulms can be used for fodder or silage. The seeds remain edible for several years, if properly stored, and are rich in protein compared with cereals. Pulses are, therefore, especially important in the native agriculture of tropical and sub-tropical regions. However, they are very prone to infestation, both in the field and after harvest, by pea and bean "weevils" of the family Bruchidae, which are prolific and rapid in their breeding and can quickly cause a serious reduction in the nutritive value of the stored seeds.

Larson (1920) estimated that in 1918 the loss from infestation of the crop of beans in California by two species of Bruchids was about 10 per cent., valued at over $4,000,000. Lefèvre (1950) stored beans in the Belgian Congo for eight months after harvest and found 48–70 per cent. damaged. The same author (1953) later kept beans in sacks for 12 months by which time 95 per cent. had been holed. Lastly, Cockbill (1953) in Southern Rhodesia recorded a loss in weight of 13·3 per cent. ascribable to Bruchid damage in a stack of one hundred sacks each containing 200 lb. of beans, which had been stored for five months. With these figures for percentage of holed beans in mind, it is interesting to note that a French decree of 20th February 1946 held that the presence of five per cent. or more of damaged beans rendered the parcel unfit for human consumption and that such infested lots must be treated by the owner to ensure total destruction of the insects. A decree promulgated in Madagascar on 26th August 1948 prohibited the export of beans, etc., containing active infestation and required disinfestation by vacuum fumigation or by a dust, without toxic risk to man. There is no doubt, therefore, of the economic importance of Bruchid infestation in pulses.

During recent years interest has developed in certain parts of East and Central Africa in growing peas and beans for export to the United Kingdom, partly for canning (haricot type only) and partly for seed. For either of these purposes clean, uninfested seed is essential and the chief obstacle in its production is infestation by the Bruchids, *Acanthoscelides obtectus* (Say) and *Callosobruchus chinensis* (L.). Importers in the United Kingdom object to the presence of insects, dead or alive, among or inside the seeds and to the typical so-called "windows" made by the larvae just before pupation. It has been suggested that, instead of the present 4,000–5,000 tons, some 35,000 tons per annum of suitable beans from East Africa could be absorbed in the U.K. market, especially for canning, if the crop could be protected against Bruchid infestation.

On his return from a visit to the East African Territories in 1952, Mr. D. W. Hall, Colonial Liaison Officer at the Pest Infestation Laboratory, urged that research should be directed to the prevention of Bruchid infestation of peas, cowpeas and beans for local consumption and, especially, to the protection of haricot-type beans grown for export to the United Kingdom. This paper gives an account of the ensuing investigations. No experimental work has been done on the reduction of infestation in the crop before harvest, as that is beyond the scope of the work of the Pest Infestation Laboratory.

Much of the literature on the control of Bruchids in stored products concerns the use of fumigants. Although they penetrate well and kill insects quickly, the need for special skill and care in the use of toxic gases restricts their applicability in Colonial Territories, and the lack of residual protection leaves the product open to immediate reinfestation. Moreover, in the Colonies, part of the growing and storing of pulses is in native hands and insects must be dealt with by means that are cheap, easily applied, and relatively free from hazard. These conditions are best met by the use of insecticidal dusts.

Cockbill (1953) has shown that considerable reduction of losses can be achieved by a cheap external treatment of sacks of beans with BHC dust. The value of such treatment would, however, be greatly reduced or retreatment would be necessary if the sacks should be moved from time to time, as happens in the sequence of trade from grower to exporter. There would clearly be advantages in mixing the insecticidal dust with the product, provided that control of the insects could be effected at levels of dosage near the acceptable tolerance limits for man and animals. In planning the experimental work described in the present paper, particular attention was therefore paid to admixture with peas and beans of inert mineral dusts, and of dusts containing DDT or BHC at dosages related to the tolerance limits. Certain special contact insecticides available in East Africa were examined first and then various materials more easily available in other territories.

The earliest recommendations on dusts for control of Bruchids in beans depended on mechanical protection of the product with heavy doses of admixed clays, ashes, hydrated lime, talc or sand (Metcalf, 1917; Headlee, 1924; Subramaniam, 1935; Deay & Amos, 1936; Lever, 1941).

Another group of recommendations concerns the admixture with peas and beans of smaller quantities of dusts which have a physical action on the insect and are generally described as "inert dusts". Those which have been tested against various species of Bruchids and recommended for use in dry climates at dosages ranging from 0·5 to 2 per cent. by weight include silica, magnesite, bentonite, rock phosphate, anhydrite (Chiu, 1939; Morgan & Pasfield, 1942; Friend, 1945; Cannon, 1946; Janjua & Nasir, 1948; Chatterji, 1953).

A considerable number of authors recommend the admixture of DDT dusts at dosages ranging from about 20 to 2,000 p.p.m. of technical DDT on the beans (Friend, 1945; Friend & Pasfield, 1945; Hely, 1945; Van den Bruel, 1946; Cannon, 1946; Aboim, 1948; Oosthuisen, 1948; Horber, 1950; Lefèvre, 1950, 1953). Although Lefèvre used 50–100 p.p.m. DDT very effectively in his trials with bagged beans, he presents evidence showing that more than 90 per cent. of DDT added to beans was lost by entrainment in the steam during cooking. Smaller doses of DDT have been suggested by a few authors, *viz.*: 10 p.p.m. by Chatterji (1953); 6 p.p.m. by Lepage & Giannotti (1944); 2 p.p.m. by Janjua & Nasir (1948).

In compiling figures for dosages of γ BHC, it has been assumed that reference in the literature to technical or crude BHC implies the use of a product containing about 12·5 per cent. of the γ isomer. Recommendations cover the range from 0·25 to 12·5 p.p.m. γ BHC to be admixed with the beans, etc. (Aboim & Veiga-Ferreira, 1948; Van den Bruel, 1946; Janjua & Nasir, 1948; Oosthuisen, 1948; Chatterji, 1953).

It will thus be seen that suggested doses of DDT and BHC have covered an extraordinarily wide range and a re-investigation of the situation was called for, particularly if the product is intended for consumption. This has been covered in the present experimental work.

Culture of the Test Insects.

Two species of the family Bruchidae are of outstanding economic importance, because they have been widely spread by commerce, can attack seeds in the pod before harvest, and can continue to multiply in the dried and stored seeds. These two are the Bean Beetle, *Acanthoscelides obtectus*, and the Cowpea Beetle, *Callosobruchus chinensis*. These were, therefore, used in the experimental work to be described.

A healthy strain of *C. chinensis* was available from the Laboratory's insectaries and a stock of *A. obtectus* was bred from adults out of a sample of mixed beans newly arrived from Tanganyika. The first task was to establish a procedure for culturing the insects under standardised conditions so as to produce beetles of known age in a steady and sufficient supply for experimental purposes. Some time had therefore to be spent in preliminary investigations of breeding methods. The length of life of the adults under conditions of starvation was also determined.

C. chinensis could not be cultured successfully on red kidney or white haricot beans, but reproduced prolifically at 25°C. and 70 per cent. R.H. on round, green peas, the life-cycle requiring about five weeks. The eggs are stuck firmly to the surface of the peas and the young larva bites its way directly into the pea through the underside of the egg. It is probable that the adult does not feed, but starvation tests at 25°C. and 70 per cent. R.H. showed that the first beetles died on the 5th day after emergence, 50 per cent. died by the 11th day, and 100 per cent. by the 19th day.

A. obtectus could not be reared successfully on red kidney beans or peas, but was able to breed in white haricot beans. It was not so prolific as *C. chinensis* and was therefore cultured at 30°C. and 70 per cent. R.H., the life-cycle under these conditions also requiring five weeks. The eggs are laid loosely among the beans and the young larva crawls about for a time seeking a suitable place at which to bore its way in. During starvation tests at 25°C. and 70 per cent. R.H., the first beetles died on the 8th day, 50 per cent. died by the 22nd day, and 100 per cent. by the 36th day.

Susceptibility of the Beetles to BHC Vapour.

The insecticides most easily available in East Africa were said to be powders comprising crude BHC on a local diatomite and all the preliminary experiments

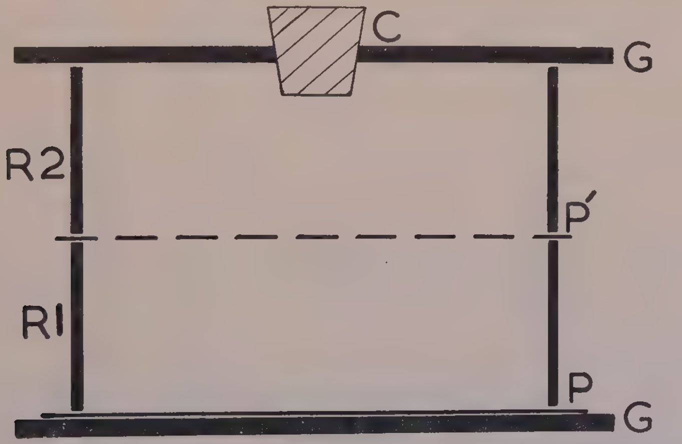


Fig. 1.—Apparatus used to determine the effect of γ BHC vapour on beetles. C = cork; G = glass plate; P = filter paper; P′ = perforated filter paper; R1, R2 = glass rings.

were designed to enable a recommendation to be made for the use of this type of preparation, provided that it proved suitable, at the earliest possible moment. To establish quickly whether there was a major difference in susceptibility of the two species of beetles to γ BHC, their reaction was observed during confinement in an atmosphere saturated with the BHC vapour.

A glass ring, 2 cm. high, 6 cm. across, and with both ends ground flat, was stood on a 7 cm. Whatman no. 1 filter paper resting, in turn, on a glass plate (see fig. 1). On the filter paper was placed centrally 0·1 gm. of a dust containing 0·05 per cent. γ BHC in diatomite to act as the source of insecticide vapour. A second filter paper, perforated about 50 times with a pin, was laid on the top of the ring and surmounted by a second ring. The unit was closed by an upper glass or perspex plate, with a central corked hole 1 cm. in diameter, and held together by rubber bands. After three days at 25°C. and 70 per cent. R.H. to allow time for generation and diffusion of the γ-BHC vapour, the cork was gently withdrawn and 30 beetles dropped through the hole by means of a small funnel. The cork was quickly reinserted and the fate of the beetles observed at intervals through the cover with the aid of a binocular microscope. An insect was considered "knocked down" if it lay on its back unable to regain the normal position, or if it remained on its feet but had clearly lost co-ordination of locomotory movements. It was considered dead if it showed no spontaneous movement nor, at the final examination, any reflex movement when touched with a brush. The insects counted as knocked down therefore included those dead.

The percentages of beetles knocked down (K-D) or killed were derived from three replicates of 30 beetles, 1–3 days old, exposed to the vapour and two replicates of 30 beetles as controls. The results are summarised in Table I.

TABLE I.

The effect of γ BHC vapour upon adults of *C. chinensis* and *A. obtectus* at 25°C. and 70 per cent. R.H.

	16 hr.		24 hr.		48 hr.		72 hr.		96 hr.	
	K-D%	Kill %	K-D %	Kill %	K-D %	Kill %	K-D %	Kill %	K-D %	Kill %
				C. chinensis						
Treated ..	10	6	64	6	96	27	100	74	100	81
Control ..	0	0	1	1	7	7	8	8	16	16
				A. obtectus						
Treated ..	1	0	6	0	10	3	18	7	34	10
Control ..	0	0	0	0	0	0	0	0	0	0

The results show clearly that adults of *A. obtectus* are considerably more resistant to BHC vapour than *C. chinensis*, and that a majority of the latter are seriously affected within 24 hr.

Jar Tests with BHC-diatomite Dusts.

Beans and peas were shaken with different quantities of Kenya diatomite dust (grade K) stated to contain 0·05 per cent. γ BHC (as crude BHC). The minimum dosage which would give reasonably uniform coverage was found to be 0·01 per cent. of the weight of the seeds; the maximum adherence was reached at about 0·05 per cent. Dosing at 0·1 per cent. showed a slight visible excess of non-adherent dust. The last dosage rate is equivalent to the addition of 3·2 oz. of dust per 200 lb. of seeds (100 gm. per 100 kg.).

With the above figures in mind peas and beans were dusted with diatomite containing 0·05 or 0·025 per cent. γ BHC, and with the diatomite base (grade K) alone, each at dosages of 0·05 and 0·01 per cent. by weight. Lots of 150 gm. of the peas, in glass jars with muslin tops, were infested by the addition of 40 adult *C. chinensis*, 0–4 days old, and kept at 25°C. and 70 per cent. R.H. Similar lots of the beans were infested by the addition of 40 adult *A. obtectus*, 0–4 days old, and kept at 30°C. and 70 per cent. R.H. Two replicates were set up for each combination of dust and level of dosage. One was examined for knockdown and kill of the beetles after three days and the other after six days, all beetles being returned to the jars. All jars were examined again after seven and nine weeks to determine the total F_1 emergence. The results are summarised in Table II.

TABLE II.

The effect of various concentrations of two BHC dusts upon infestation of peas and beans by 40 beetles.

Dust	Concn. % by wt.	γ BHC p.p.m.	3 days		6 days		F_1 Emergence*
			K-D%	Kill %	K-D %	Kill %	
		C. chinensis on peas at 25°C. and 70% R.H.					
0·05% γ BHC on diatomite	0·05	0·25	100	100	100	100	0
	0·01	0·05	80	65	100	100	24
0·025% γ BHC on diatomite	0·05	0·125	100	98	100	100	0
	0·01	0·025	40	15	100	100	84
Diatomite (K)	0·05	—	95	88	100	100	30
	0·01	—	10	10	70	18	177
Not dusted	—	—	18	3	43	25	190
		A. obtectus on beans at 30°C. and 70% R.H.					
0·05% γ BHC on diatomite	0·05	0·25	100	63	100	93	0
	0·01	0·05	100	0	100	13	8
0·025% γ BHC on diatomite	0·05	0·125	100	48	100	83	0
	0·01	0·025	90	5	98	10	33
Diatomite (K)	0·05	—	38	3	83	20	12
	0·01	—	90	5	100	38	3
Not dusted	—	—	0	0	8	8	580

* Mean of two replicates.

In spite of the unexpectedly small F_1 emergence of *C. chinensis* from the controls and one or two anomalous results obtained with *A. obtectus*, Table II shows clearly that the addition of 0·05 per cent. by weight of diatomite alone to peas or beans is sufficient to reduce very markedly the reproductive potential of both species of beetles and that the addition of γ BHC to the diatomite to give an eventual concentration of 0·125 p.p.m. in the seeds is sufficient to prevent reproduction by both species. In conformity with the conclusion drawn from the vapour-exposure tests, *A. obtectus* proved more resistant to the γ-BHC dusts than *C. chinensis*, yet, in spite of the very low percentage kill of the former with 0·025–0·05 p.p.m. γ BHC, there were very few progeny. The explanation is doubtless that adults of *A. obtectus* lay eggs loosely among the beans, so that the newly emerged larvae, whilst searching for a suitable spot at which to penetrate the testa, are exposed to the action of the insecticide and to the difficulties of climbing over and gnawing at dusted beans: larvae of *C. chinensis* are not exposed to these hazards.

Sacklet Test with BHC-diatomite Dust.

Gamma BHC is known to be very toxic in the vapour phase and the tests done in the glass jars were clearly made under conditions conducive to nearly the maximal effect of the vapour, an effect which might be considerably reduced in practice as a result of ventilation. An attempt was therefore made to approach a little nearer to practical conditions. Small sacks, 6 in. by 4·5 in., were made from hessian jute sacking (weighing about 9 oz. per sq. yd.) and filled with peas (approx. 540 gm.). The peas were untreated; or mixed with 0·025, 0·05, 0·1, or 0·2 per cent. of the dust comprising 0·05 per cent. γ BHC on diatomite; or mixed with 0·025 or 0·05 per cent. of the dust comprising 0·025 per cent. of γ BHC on diatomite. The series was replicated twice. After adding 150 adults of *C. chinensis*, 0–4 days old, the sacklets were sewn up and kept in a room maintained at 25°C. and 70 per cent. R.H. *A. obtectus* was not included in this test in view of the greater effect of the dust on its reproductive potential. At first the sacklets were kept together in a wire-gauze cage, but a few parent beetles managed to escape through the meshes of the hessian and it became evident that counts of the F_1 generation in each sacklet could not be accurate. Each sacklet was therefore separately covered with a wire-gauze envelope (20 meshes per inch) to prevent dispersal of the beetles. To avoid the accumulation of insecticidal vapour, the sacklets were stood on a metal tray close to the air-outlet duct from the constant temperature room. After 6–7 weeks the beetles in each sacklet were removed and counted: a second count was made 9 weeks from the start, just before the expected commencement of emergence of the F_2 generation. The number of parent beetles (150) was subtracted in arriving at the total F_1 emergences recorded in Table III.

The control exercised by the dust under these conditions was not so good as in the jar tests. About 0·025 per cent. of the 0·05 per cent. γ BHC in

TABLE III.

The effect of γ BHC on diatomite in protecting peas in small sacks against infestation by *C. chinensis*.

Concn. of γ BHC in dust %	Concn. of dust in peas %	Concn. of γ BHC in peas p.p.m.	F_1 emergence*
0·05	0·2	1·0	14
	0·1	0·5	24
	0·05	0·25	68
	0·025	0·125	107
0·025	0·05	0·125	168
	0·025	0·0625	293
0	0	0	1023

* Mean of two replicates.
150 beetles added: 25°C. and 70 per cent. R.H.

diatomite (or 0·05 per cent. of the 0·025 per cent. dust) was needed to prevent the infestation from increasing, but eight times this concentration did not entirely prevent breeding. This must have been due to a few of the females laying one or two eggs immediately on introduction into the sacklet before the insecticidal dust had time to affect them, a circumstance perhaps helped by a small proportion of the beetles quickly finding their way to the outside peas next to the sacking where the concentration of γ-BHC vapour was probably slightly lower because of ventilation. The latter idea is supported by the fact that the newly emerging larvae were not killed, as they would have been in an atmosphere saturated with the vapour.

In view of the urgency of the problem, a recommendation was made at this stage to the East African Territories that they should protect beans, etc., in store against infestation by *Callosobruchus* and *Acanthoscelides* by the admixture with each 200 lb. of beans of 6 oz. of a dust comprising 0·05 per cent. lindane (99–100 per cent. γ BHC) on Kenya diatomite. This rate of admixture corresponds to 0·94 p.p.m. γ BHC on the beans, which gives a reasonable safety margin in treatment without too much loose dust among the product yet remains within the limit of 1 p.p.m. γ BHC acceptable to the Kenya authorities and to the U.K. importers and processors.

Tests with Inert Dusts.

In view of the good results obtained with diatomite (grade K), without the addition of BHC, further tests were done to determine the value of various grades of East African diatomites. In addition, a few other types of inert dusts were investigated because diatomite is not generally available in British Colonial Territories.

Jar tests with different diatomite dusts.

Enquiries were made for samples of one or two of the different grades of diatomites suitable for use in insecticides which were available from each of the two known deposits in Kenya. A special attempt was made to obtain commercially available powders of small particle size because, from information about the relation between particle size and insecticidal efficiency of other mineral dusts (Parkin, 1944), they could be expected to be more effective. Samples were obtained from the two sources in Kenya but, as the species of diatoms in them were so different and the microscopically observed degrees of fragmentation were so much at variance with what was expected from the commercial descriptions, an objective method of comparison was sought. Each

TABLE IV.

Percentages by weight of component fractions of diatomite dusts.

Sample	Coarse	Medium	Fine
K	53	29	18
K (ground)	22	28	50
F 57K ..	22	43	35
F 80 ..	37	46	17
RM ..	41	36	23
RMP ..	31	46	23

material was therefore divided into three fractions by sedimentation in absolute ethyl alcohol in an Atterberg cylinder for periods of 0·25 and 4·25 hr. These fractions are called coarse, medium and fine in Table IV. Their ranges of particle size cannot be calculated as the diatoms and their fragments are flat plates and not spheres but, had the particles been spherical, the sedimentation conditions would have corresponded to the following sizes:— coarse = $> 19\mu$, medium = $19–4{\cdot}8\mu$, fine = $< 4{\cdot}8\mu$.

Grade K is a relatively coarse grade of diatomite and was the carrier employed in the locally produced 0·05 per cent. γ-BHC dust. This diatomite was not used in the present series of tests as its efficacy had been determined in the earlier laboratory tests (see Table II). Grade K was used, however, after grinding to a fine particle size in a pestle and mortar. The sample F 57K was stated to be a finely ground powder (90·1 per cent. passing 325 mesh and 99·75 per cent. passing 200 mesh) and F 80 a separated powder (90·6 per cent. passing 325 mesh and 98·1 per cent. passing 200 mesh) from the same deposits. The sample RM was from a different deposit and was said to have been reduced in a hammer mill until 97·5 per cent. passed a 200-mesh screen. Sample RMP was similar in origin to RM but was stated to have been passed through a micro-pulveriser and tested to pass a 300-mesh screen.

Using the jar test technique already described, peas were dusted with 0·4, 0·2 and 0·1 per cent. by weight of the various dusts and exposed to *C. chinensis*. Similarly, haricot beans were dusted with 0·1, 0·05 and 0·025 per cent. of the dusts and exposed to *A. obtectus*. The summarised results with *C. chinensis* are given in Table V, and with *A. obtectus* in Table VI.

Comparison of Tables IV, V and VI shows that the diatomite dusts were generally the more effective in preventing infestation the smaller their particle

TABLE V.

The effect of mixing dried peas with various concentrations of different diatomite dusts upon infestation by *C. chinensis*.

Grade	Concn. % by wt.	Kill (%) 3 days	Kill (%) 6 days	F_1 emergence*
K (ground)	0·4	100	100	0
	0·2	100	100	6
	0·1	100	100	23
F 57K	0·4	100	100	9
	0·2	100	100	24
	0·1	100	100	55
F 80	0·4	100	100	25
	0·2	98	100	36
	0·1	95	100	71
RM	0·4	98	100	61
	0·2	95	100	96
	0·1	88	100	364
RMP	0·4	100	100	3
	0·2	100	100	4
	0·1	98	100	57
Control	0	8	38	650

* Mean of two replicates.
40 beetles added; jars kept at 25°C. and 70 per cent. R.H.

size: other differences appeared to be unimportant. By comparison of the data for applications of 0·1 per cent. of the dusts (see Tables V and VI), it is clear that adults of *C. chinensis* are much more susceptible to the lethal effects of the dusts than those of *A. obtectus*, yet at least four times as much dust is required to prevent reproduction, as measured by F_1 emergence, by *C. chinensis* than by *A. obtectus*. This is doubtless bound up with the difference in egg-laying habits of the two species of beetle and the consequent exposure of the susceptible first-stage larvae of *A. obtectus* to the dusts, as was noted in the BHC-dust tests. From the practical viewpoint, both beetles should be controlled by the admixture of 6–12 oz. per 200 lb. bag of peas or beans (admixture of 0·2–0·4 per cent. by weight) of a diatomite dust of fine particle size, provided that the relative humidity of the ambient atmosphere does not exceed 70 per cent., since the efficacy of inert mineral dusts is very dependent on this factor (Parkin, 1944). The particle size must be considerably smaller than that of diatomite K, the base used in the BHC-diatomite dust already tested: the frustules should be finely fragmented.

TABLE VI.

The effect of mixing haricot beans with various concentrations of different diatomite dusts upon infestation by *A. obtectus*.

Grade	Concn. % by wt.	Kill (%) 3 days	Kill (%) 6 days	F_1 emergence*
K (ground)	0·1	98	98	0
	0·05	65	88	0
	0·025	38	65	7
F 57K	0·1	25	75	0
	0·05	3	35	46
	0·025	15	50	46
F 80	0·1	55	63	0
	0·05	40	35	2
	0·025	18	38	126
RM	0·1	38	63	1
	0·05	15	38	94
	0·025	18	25	531
RMP	0·1	60	95	0
	0·05	45	93	1
	0·025	45	53	42
Control	0	9	22	864

* Mean of two replicates.
40 beetles added; jars kept at 30°C. and 70 per cent. R.H.

Jar tests with other inert dusts.

Five dusts, other than diatomite, were selected for investigation. A colloidal silica powder of very small particle size (about 1μ) and a similar colloidal aluminium pentasilicate powder were included because of their known efficiency for control of some species of stored-product insects and because the aluminium silicate had been claimed to be successful in preventing beetle infestation of haricot beans in Madagascar. A well-known commercial preparation of ground rock phosphate and sulphur was included because of its widespread use in Near Eastern areas for the protection of grain against weevil. Kaolin and talc were also included because of their ready availability and frequent use as bases for dusts incorporating chemical insecticides such as BHC and DDT.

The technique of the jar test followed that already described. The concentrations of the dusts are given and the results are summarised in Tables VII and VIII.

The silica powder gave outstandingly good control of both species of beetle and was superior in its effectiveness to the aluminium silicate. The latter is commercially recommended for use at a dosage of 7 oz. per 2 cwt. of produce, *i.e.*, 6·3 oz. per 200 lb. of beans and this corresponds to a concentration of 0·2 per cent. by weight. It can be seen in Tables VII and VIII that this rate of dosage is more than enough for *A. obtectus* but marginal for *C. chinensis*. On the other hand, the greater efficacy of the silica might be partly wasted under practical conditions because of the difficulty of making a reasonably uniform mixture of only 3·2 oz. of dust in 200 lb. of beans, the 0·1 per cent. level of treatment.

Rock phosphate was very effective against *A. obtectus* at concentrations down to 0·1 per cent. but did not give reliable protection against *C. chinensis* even at 0·8 per cent.

Kaolin did not sufficiently control reproduction of *A. obtectus* at dosages of 0·4 per cent. or less and failed to control *C. chinensis* at 0·8 per cent.

Talc failed to control either species at 0·8 per cent.

TABLE VII.

The effect of mixing dried peas with various concentrations of five inert dusts upon infestation by *C. chinensis*.

	Concn. % by wt.	3 days		6 days		F_1 emergence*
		K-D %	Kill %	K-D %	Kill %	
Silica	0·4	100	100	100	100	0
	0·2	100	100	100	100	0
	0·1	100	100	100	100	3
	0	10	0	30	10	451
Aluminium silicate	0·4	100	100	100	100	5
	0·2	100	100	100	100	26
	0·1	100	100	100	100	83
	0·05	98	93	100	100	114
	0·025	83	80	100	100	192
	0	5	3	25	13	689
Rock phosphate	0·8	100	100	100	100	42
	0·4	100	100	100	100	65
	0·2	100	100	100	100	116
	0·1	95	95	100	100	84
	0	3	3	48	48	793
Kaolin	0·8	80	65	100	95	252
	0·4	70	65	100	80	350
	0·2	55	45	98	68	459
	0·1	23	13	90	43	1130
	0	3	3	20	0	551
Talc ..	0·8	3	0	63	20	311
	0·4	0	0	20	0	577
	0·2	33	3	40	10	394
	0·1	3	3	30	13	502
	0	8	0	8	0	697

* Mean of two replicates.
40 beetles added; jars kept at 25°C. and 70 per cent. R.H.

The five dusts therefore performed as expected on the basis of existing knowledge of the properties of inert mineral dusts. With the doubtful exception of the rock phosphate mixture, these materials are bland and unlikely to arouse any toxic symptoms on ingestion; indeed some are used medicinally. As pointed out for the five diatomite dusts, however, they are subject to a progressive reduction in their insecticidal efficiency as the relative humidity of the ambient atmosphere rises above about 75 per cent. Nevertheless, there are many parts of the tropics and sub-tropics where the relative humidity would be favourable.

TABLE VIII.

The effect of mixing haricot beans with various concentrations of five inert dusts upon infestation by *A. obtectus*.

Dust	Concn. % by wt.	3 days		6 days		F_1 emergence*
		K-D %	Kill %	K-D %	Kill %	
Silica	0·1	100	100	100	100	0
	0·05	100	98	100	95	0
	0·025	93	80	90	90	0
	0	23	10	58	55	143
Aluminium silicate	0·4	100	88	100	100	0
	0·2	100	83	100	100	0
	0·1	95	80	100	98	0
	0·05	73	38	90	78	4
	0·025	48	25	65	53	10
	0	0	0	15	5	793
Rock phosphate	0·8	100	95	100	100	0
	0·4	95	93	100	100	0
	0·2	100	93	100	100	0
	0·1	98	93	100	100	0
	0	3	3	45	38	789
Kaolin	0·8	80	73	90	90	1
	0·4	50	3	65	45	53
	0·2	28	20	55	40	152
	0·1	5	5	20	8	308
	0	0	0	15	10	634
Talc	0·8	5	3	20	3	186
	0·4	5	3	15	8	288
	0·2	8	0	13	0	273
	0·1	0	0	8	0	353
	0	0	0	8	0	380

* Mean of two replicates.

40 beetles added; jars kept at 30°C. and 70 per cent. R.H.

Jar Tests with BHC on Kaolin.

Because of the lack of availability in many colonial territories of diatomite as a base for insecticidal dusts, experiments were made to assess the effect of a dust comprising BHC on a base with no significant inherent insecticidal toxicity. Gamma BHC in solution in benzene was therefore mixed with kaolin and the solvent evaporated to leave a dust containing 0·05 per cent. of the BHC. The usual type of jar test was done with both species of beetles (see Table IX).

Comparison of Tables II and IX shows that the γ BHC was as effective on kaolin as on diatomite, but comparison of Tables II, VII and VIII reminds one that, as the BHC volatilises, the diatomite will give much better protection than the kaolin.

TABLE IX.

The effect of 0·05 per cent. γ BHC on kaolin upon infestation of peas and beans by Bruchids.

Concn. % by wt.	γ BHC p.p.m.	3 days K-D %	3 days Kill %	6 days K-D %	6 days Kill %	F_1 emergence*
		C. chinensis on peas at 25°C. and 70% R.H.				
0·1	0·5	100	100	100	100	0
0·05	0·25	100	100	100	100	0
0·025	0·125	100	100	100	100	0
0	—	18	8	45	10	190
		A. obtectus on beans at 30°C. and 70% R.H.				
0·1	0·5	100	100	100	100	0
0.05	0·25	100	100	100	100	0
0·025	0·125	100	90	100	100	0
0	—	3	3	0	0	699

* Mean of two replicates.
Jar test: 40 beetles added.

Jar Tests with DDT Dust.

Having shown in laboratory tests that γ BHC on diatomite or kaolin was effective in controlling the two species of Bruchids at a dosage which did not exceed the tolerance limit of 1 p.p.m. γ BHC at present operative in Kenya, a test was made of the value of DDT at dosages related to its tolerance limit in the United Kingdom of 7 p.p.m. of the p,p′isomer. The usual experimental technique was used employing dusts containing 1·4 per cent. p,p′DDT on diatomite or kaolin. The diatomite-based dust was made by dilution of a

TABLE X.

The effect of 1·4 per cent. DDT on diatomite or kaolin upon infestation of peas and beans by Bruchids.

Dust base	Concn. % by wt.	DDT p.p.m.	3 days K-D %	3 days Kill %	6 days K-D %	6 days Kill %	F_1 emergence*
			C. chinensis on peas at 25°C. and 70% R.H.				
Diatomite	0·1	14	100	100	100	100	0
	0·05	7	100	100	100	100	0
	0·025	3·5	100	100	100	100	15
	0	—	23	20	38	35	279
Kaolin	0·1	14	100	100	100	100	0
	0·05	7	100	100	100	100	2
	0·025	3·5	100	93	100	100	66
	0	—	3	3	30	20	146
			A. obtectus on beans at 30°C. and 70% R.H.				
Diatomite	0·1	14	100	100	100	100	0
	0·05	7	100	100	100	100	0
	0·025	3·5	100	100	100	100	0
	0	—	43	25	45	36	784
Kaolin	0·1	14	100	100	100	100	0
	0·05	7	100	100	100	100	1
	0·025	3·5	20	20	90	78	188
	0	—	10	10	37	37	824

* Mean of two replicates.
Jar test: 40 beetles added.

commercial diatomite dust containing 5 per cent. of technical DDT (assumed to be 75 per cent. pure) with a similar grade (grade K) of diatomite; the kaolin-based dust was prepared by impregnation of the kaolin with pure DDT in benzene solution and evaporating to dryness. The results are shown in Table X.

On the slight evidence available from comparison of the figures for knock-down and kill at 3·5 p.p.m. dosage level on the kaolin base, adults of *A. obtectus* are somewhat more resistant to DDT than *C. chinensis*, a result in agreement with other data (Parkin, 1953). Comparison of F_1 emergences discloses a tendency for the dusts to be less effective against *C. chinensis*. With both species, diatomite proved a better base for the DDT dust than kaolin, indicating, for the diatomite, a combined action of chemical insecticide and mineral base. Peas and beans were protected against infestation by 7 p.p.m. DDT on diatomite or kaolin and, since this insecticide is much more persistent than γ BHC, it is likely that this rate of dosage would be sufficient in practice.

In the foregoing test, the F_1 emergences of *C. chinensis* from the untreated peas were unexpectedly low and no cause was evident, especially as the natural mortality was reasonable for this species.

Sacklet Test with DDT Dust.

A sacklet experiment with *C. chinensis*, similar to that using BHC, was done with peas treated with DDT dusts. Dusts were made by the solvent evaporation method to comprise 0·35 per cent. pure DDT on kaolin or diatomite (grade RMP) and were carefully mixed at 0·2 and 0·4 per cent. by weight with the peas, which thus contained 7 or 14 p.p.m. All treatments were duplicated. The results are summarised in Table XI.

TABLE XI.

The effect of 0·35 per cent. DDT dusts in protecting peas in small sacks against infestation by *C. chinensis*.

Dust base	Concn. of dust in peas %	Concn. of DDT in peas p.p.m.	F_1 emergence*
Diatomite	0·4	14	0
	0·2	7	7
Kaolin	0·4	14	13
	0·2	7	20
—	0	0	1095

* Mean of two replicates.
150 beetles added: 25°C. and 70 per cent. R.H.

The results with DDT were similar to those with γ BHC at the corresponding recommended dosages, namely 7 p.p.m. and about 1 p.p.m. As expected, DDT on the diatomite was slightly superior to DDT on kaolin.

Discussion.

This experimental work has clearly shown that the assessment of the relative resistance to insecticides of *C. chinensis* and *A. obtectus* depends upon the criterion of toxicity employed, a feature reported before from work on other insects (Parkin, 1951). Since the present investigation had a practical objective, the prevention of breeding seemed more important than rapid kill of adult beetles; a combination of the two would clearly be advantageous, as the layman is chiefly impressed by the latter. It is interesting to note in this connection that adults of *A. obtectus* were in general considerably more resistant to insecticidal dusts than those of *C. chinensis*, yet the reproductive cycle of the former is the more easily interrupted, presumably because newly hatched larvae of *A. obtectus* are so vulnerable. Fortunately, however, the two species proved so susceptible, to both physically and chemically active insecticidal dusts, as to lead to optimism about their control in practice. Nevertheless, a disadvantage of the dust treatment is that, with the doubtful exception of those incorporating γ BHC, the dusts have no effect upon immature stages within the peas and beans, so the damage must be expected to increase slightly during maturation of the larvae. Such a slight increase should be of no practical significance compared with the value of the subsequent lethal and protective effects of the treatment.

The rate of dosage needs to be considered carefully because enough dust must be used to ensure reasonably uniform distribution throughout the product, yet an excess must be avoided as being wasteful, detrimental to the appearance of the product, and troublesome in eventual removal, especially if the insecticide also has significant mammalian toxicity. However, the considerations governing the dosage for seed are less stringent because the value of the product is higher and there is no need for eventual removal of the dust: germination will not be affected by reasonable doses that are fully adequate to protect against insect infestation.

Securing reasonably uniform admixture of the dust can be a very real problem in practice when seed-dressing machines, tumbling drums, etc., are not available. Only two methods are likely to be used by a native grower, mixing by shovel or application by "pepper-pot". When mixing by shovel the requisite amount of dust is spread over the surface of a heap of beans on the floor and the heap is shovelled to a new position; it is then shovelled into sacks. Using grain as the product to be treated, this double shovelling has been found the minimum effort to give a good mix. In the "pepper-pot" method, the beans are continuously dusted by a separate worker who shakes in the mouth of the sack a tin, suitably perforated at the lower end, containing the required amount of dust as the beans are shovelled or tipped into the sack. In rough trials with grain the shovelling method gave markedly better distribution.

A sack of beans commonly contains 200 lb. and, for this quantity, the minimum dose of insecticidal dust has been tentatively set at 6–8 oz. (about 200 gm. per 100 kg.). From the information and experience at present available

TABLE XII.

Assessment of the practical value of the dusts tested on the basis of the dosage at 6·4 oz. per 200 lb.

Dust	Test Method	*C. chinensis* F_1 per 40 beetles	Assessment
Silica	Jar	0	Excellent
Aluminium pentasilicate ..	,,	26	Satisfactory
Diatomite (finely ground) ..	,,	24	Satisfactory
Rock phosphate	,,	116	Failed
Kaolin	,,	459	Failed
Talc	,,	394	Failed
0·05% γ BHC on diatomite	Sacklet	4	Very good
0·05% γ BHC on kaolin	Jar	0	Very good
0·5% tech. DDT on diatomite	Sacklet	2	Very good
0·5% tech. DDT on kaolin ..	,,	7	Very good

this should give sufficient dust for mixing in by the simple procedure described above and will carry the chemical insecticides at practicable concentrations. More dust will be applied than can adhere to the product, but the slight excess is an essential part of the treatment and must not be removed until the desired period of protection has ended.

The various insecticidal dusts used in the tests are listed in Table XII, together with the numbers of F_1 adults of *C. chinensis* recorded when peas were mixed with 0·2 per cent. by weight of each dust (6·4 oz. per 200 lb.) and exposed to an initial infestation of 40 beetles (see previous Tables). The efficacy of the dusts is also tentatively assessed in general terms on the basis of the suggested practical dosage level of 6–8 oz. per 200 lb.

Where the relative humidity is not too high for the use of an inert dust of moderate efficiency and finely ground diatomite is available, this is likely to be the insecticidal dust of choice for the protection of peas and beans. The commercial preparation of colloidal silica was so effective at 70 per cent. relative humidity that it is possible that it would still perform satisfactorily at humidities up to 80 per cent. or more. Such a dust would cost 8–10 times as much as the diatomite but, even so, the cost of the dust for a 200 lb. bag of beans (valued at perhaps £3) should not exceed sixpence. The commercial preparation of colloidal aluminium silicate would probably cost about twice as much. The diatomite-based DDT and BHC (which should be of lindane quality) would clearly be more expensive than the diatomite alone, but these dusts would not be recommended except where diatomite is easily available: the addition of the chemical insecticide greatly increases the effectiveness of the dust and permits the use of a coarser grade of diatomite. DDT and BHC may also be used effectively on a kaolin base and in many parts of the world these dusts would be the cheapest form of treatment. The DDT dust is to be preferred if the protection is required for an extended period. Gamma BHC is markedly volatile at tropical temperatures and rather transient in effect, and is therefore best compounded with an inert mineral dust like diatomite. The loss of γ BHC by volatilisation would certainly be retarded, and might be obviated, by the use of paper-lined sacks for containing the dusted beans. Such a measure should be unnecessary for DDT dusts, which are much more permanent.

If all the dust applied to the product were eaten with it, there would be no toxicological risk to the consumer, since the recommended practical dosages of DDT and γ BHC do not exceed the acceptable tolerance limits. The commodity, however, will appear somewhat dusty and is likely to be sieved or washed prior to cooking. In countries like the United Kingdom which import for canning, the normal cleaning processes will probably be adequate for removal of the dust. In a simple test carried out at the Pest Infestation Laboratory, white haricot beans were treated with the crude BHC in diatomite dust containing 0·05 per cent. of the γ isomer at the recommended rate (1 p.p.m. γ BHC on the beans) and stored for five months in a tightly stoppered jar at room temperature (20–25°C.). The beans, without cleaning, were then boiled in water and compared for taste against beans similarly stored after corresponding treatment with a 0·05 per cent. pure γ BHC on diatomite dust, or with the diatomite alone: a fourth sample of beans had no dust treatment. A test in which a dozen members of the Laboratory staff took part revealed no consistent difference in taste between the cooked samples. Although the dust formulated with crude BHC did not taint the beans, BHC dusts based on lindane (99 per cent. or more γ BHC) should be used for treatment of foodstuffs.

In conclusion, it may be said that sufficient information has now been obtained to enable efficient protection of beans and other pulses to be achieved economically by the use of inert or chemical insecticidal dusts suited to a variety of local conditions. There remain the local administrative problems of distribution of suitable dusts to the growers and merchants and education of all concerned in the correct and conscientious application of the dusts in order to reap their undoubted economic benefit in terms of more food for local consumption and more for export. Alternatively, it may be necessary to consider ways in which the native grower can be encouraged to sell his surplus crop to the government agencies soon after harvest, so that it can then be properly treated and stored.

Summary.

Laboratory tests are described for determining the protective value of a number of physically and chemically active insecticidal dusts against Bruchid infestation of peas and beans. *Acanthoscelides obtectus* (Say) and *Callosobruchus chinensis* (L.) were used as the test insects and were found to be very susceptible to most of the treatments tried. Adults of *A. obtectus* were in general more resistant to the treatments than those of *C. chinensis*, but the multiplication of the former species was more easily stopped, apparently because of the vulnerability of its first-stage larvae. It is concluded that protection of peas and beans can be achieved by thoroughly mixing into 200 lb. of the commodity 6–8 oz. of one of the following dusts: colloidal silica, colloidal aluminium pentasilicate, finely ground diatomite, 0·05 per cent. γ BHC (as lindane) on diatomite or kaolin, 0·5 per cent. technical DDT on diatomite or kaolin. Rock phosphate, kaolin, or talc are not recommended. Where lindane or DDT are used in the dosages given, it is unlikely that the commodity will be tainted or rendered toxic to man or animals, even if no cleaning is undertaken.

Acknowledgements.

The authors are indebted to the following for arranging the supply of some of the insecticidal dusts for test: Dr. R. Attia, Egypt; Dr. P. Loizides, Cyprus; East African Diatomite Syndicate, Kenya; Imperial Chemical Industries (Egypt) S.A.; Kockum Diatomite, Kenya. In addition a generous sample of beans was made available by McMicken, Dixon & Hinds, Ltd., London. Some of the preliminary experimental work was done by Miss K. D. Lambe.

The investigation was carried out as part of the programme of work of the Pest Infestation Laboratory, and this account of the results is published by permission of the Department of Scientific and Industrial Research.

References.

Aboim, A. N. (1948). Action du " DDT " contre plusieurs ravageurs des denrées emmagasinées.—Bull. Soc. portug. Sci. nat., **16**, pp. 75–80.

Aboim, A. N. & Veiga-Ferreira, G. (1948). Action du " Gammexane " contre quelques ravageurs des substances emmagasinées.—Bull. Soc. portug. Sci. nat., **16**, pp. 81–93.

Cannon, R. C. (1946). Protection of stored cowpea seed against insect damage.—Qd agric. J., **63**, pp. 148–150.

Chatterji, S. (1953). On some preservatives against Bruchid pests of stored mung.—Sci. & Cult., **18**, p. 333.

Chiu, S. F. (1939). Toxicity studies of so-called " inert " materials with the Bean Weevil, *Acanthoscelides obtectus* (Say).—J. econ. Ent., **32**, pp. 240–248.

Cockbill, G. F. (1953). Investigations on the control of insect pests of stored grains and pulses.—Rhod. agric. J., **50**, pp. 294–323.

Deay, H. O. & Amos, J. M. (1936). Dust treatment for protecting beans from the Bean Weevil.—J. econ. Ent., **29,** pp. 498–501.

Friend, A. H. (1945). Experiments on the control of the Bean Seed Weevil.—J. Aust. Inst. agric. Sci., **11,** pp. 139–141.

Friend, A. H. & Pasfield, G. (1945). DDT as an insecticide. Results of preliminary trials.—Agric. Gaz. N.S.W., **56,** pp. 455–456, 467.

Headlee, T. J. (1924). Certain dusts as agents for the protection of stored seeds from insect infestation.—J. econ. Ent., **17,** pp. 298–307.

Hely, P. C. (1945). DDT as an insecticide. Result of preliminary trials.—Agric. Gaz. N.S.W., **56,** pp. 397–400.

Horber, E. (1950). Beitrag zur Biologie und Bekämpfung des Speisebohnenkäfers *Acanthoscelides obtectus* Say (Col. Bruchid.).—Mitt. schweiz. ent. Ges., **23,** pp. 233–244.

Janjua, N. A. & Nasir, M. M. (1948). Stored grain pests and their control in Baluchistan.—Bull. Dep. Agric. Baluchistan, no. 2 (1947), 32 pp.

Larson, A. O. (1920). Bean weevils in California.—Mon. Bull. Calif. Dep. Agric., **9,** pp. 344–349.

Lefèvre, P. C. (1950). *Bruchus obtectus* Say ou bruche des haricots (*Phaseolus vulgaris* L.).—Publ. Inst. nat. Étude agron. Congo belge, Sér. sci., no. 48, 65 pp.

Lefèvre, P. C. (1953). Deux insectes destructeurs des graines emmagasinées dans l'est du Congo Belge et au Ruanda-Urundi.—Bull. Inform. Inst. nat. Étude agron. Congo belge, **2,** pp. 263–268.

Lepage, H. S. & Giannotti, O. (1944). Experiências com o DDT.—Biológico, **10,** pp. 353–366.

Lever, R. J. A. W. (1941). Entomological notes. 3. Beetle pest of pulse.—Agric. J. Fiji, **12,** p. 47.

Metcalf, Z. P. (1917). Lime as an insecticide.—J. econ. Ent., **10,** pp. 74–78.

Morgan, W. L. & Pasfield, G. (1942). Dusts for protecting bean seed against *Bruchus* (*Acanthoscelides*) *obtectus* Say.—J. Aust. Inst. agric. Sci., **8,** pp. 121–122.

Oosthuizen, M. J. (1948). Seed-infesting insects.—Fmg in S. Afr., **23,** pp. 221–234.

Parkin, E. A. (1944). Control of the Granary Weevil with finely ground mineral dusts.—Ann. appl. Biol., **31,** pp. 84–88.

Parkin, E. A. (1951). Biological tests of insecticides for stored-product insects.—J. Sci. Fd Agric., **2,** pp. 136–141.

Parkin, E. A. (1953). The susceptibility to DDT dust of Coleoptera infesting stored products.—Bull. ent. Res., **44,** pp. 439–444.

Subramaniam, T. V. (1935). How to free stored grain from insect attack.—Mysore agric. Cal., 1935, p. 21.

Van den Bruel, W. E. (1946). Les méthodes de lutte utilisables contre la bruche du haricot, *Acanthoscelides obtectus* Say.—Parasitica, **2,** pp. 20–26.

INSECT INFESTATION OF WEST AFRICAN PRODUCE IMPORTED INTO BRITAIN.

By R. W. Howe and J. A. Freeman
Department of Scientific and Industrial Research,
Pest Infestation Laboratory, Slough, Bucks.

One of the duties of the Infestation Control Division of the Ministry of Agriculture, Fisheries & Food is to inspect cargoes arriving in Britain by ship for insects that may be infesting them.

Freeman (1948*a*, *b*) summarised the results of such inspection for the years 1944 to 1946. He showed that one of the chief sources of insects is produce imported from West Africa. The present paper analyses more fully the infestation record of West African produce from the commencement of inspection at the beginning of 1942 up to the end of 1952. This analysis has not been completely uniform. For the period from 1947 onwards, the data have been summarised for each month but for the earlier period each summary covered three months. The period from January 1948 has been treated in greatest detail and all the original Infestation Control Division inspection reports have been examined. Otherwise the existing quarterly analyses prepared for the papers mentioned above (Freeman, 1948*a*, *b*) have been used and the gaps remaining filled by reference to the Infestation Control Division card index. The various subjects are considered, using as long a period for each as the data allow.

Inspection and Identification.

The methods of inspection and the standards of insect infestation used are given by Freeman (1948*a*). He lists six levels of infestation. The lowest two levels are retained here, but for convenience in summarising, the remaining four are combined in pairs to give two new levels. Moderate numbers and fair numbers are combined into a category " medium ", and large numbers and very large numbers into " heavy ". Although the Infestation Control Division have ensured reasonable uniformity, it is important to emphasise that these levels refer to the insects actually *found* by inspectors, and that we do not know the relationship between numbers present and numbers visible at inspection. The various species differ in cryptic behaviour, response to disturbance, the stage of insect present and so on. Some species are readily found when present even at a low density (*Tribolium*), some are conspicuous as adults but rarely seen as larvae (*Lasioderma*), others are obvious when numerous and almost impossible to find when scarce (*Trogoderma*). Such points must be remembered when assessing the results of produce inspections.

A large proportion of the insects found must be identified on the spot, a procedure which must inevitably lead to occasional errors, especially when the insects are very abundant and include species which are difficult to separate from closely allied species without a microscope. Since, in this paper, we have attempted to correct apparent errors of identification, we must refer to these and other points of interest in identification.

Prior to 1948, *Ephestia* from West Africa were not infrequently identified as *E. elutella* (Hb.) (Freeman, 1948*a*, *b*). In 1948, Cotterell (1952) and Howe (1952) inspecting produce in Nigeria reported only *E. cautella* (Wlk.), so Mr. G. A. Brett, of the Infestation Control Division, checked all the specimens of

Ephestia collected on ships over a period of nearly a year. Only one record of *E. elutella* was made by him and there was evidence that this was due to a residual infestation.

The small number of reports of *Stegobium paniceum* (L.) which have been made have been included with *Lasioderma serricorne* (F.). These two species could not be confused in any stage in the laboratory, but this may happen in the field if inspectors do not examine specimens carefully. *Stegobium* is not known in West Africa, whereas *Lasioderma* is widespread, so it has been considered advisable to assume all these records to be *Lasioderma*.

The Nigerian form of *Trogoderma granarium* Everts bears an elytral pattern closely resembling that of *T. versicolor* (Creutz.) and as a result has sometimes been wrongly given this name.

In this summary, for various reasons, the genera *Oryzaephilus*, *Laemophloeus*, *Alphitobius*, *Carpophilus* and *Dermestes* are generally not designated to species. There has been some confusion of the species of *Oryzaephilus* because, until recently, some authorities wrongly considered that *O. mercator* (Fauv.) was merely a variety of *O. surinamensis* (L.) and not a separate species (Howe, 1953). Identification of *Oryzaephilus* collected on ships has shown that *O. mercator* is usually associated with oil seeds and *O. surinamensis* with cereals. Of the West African specimens checked by one of us (R. W. H.), 35 records were *O. mercator*, and 2, from palm kernels, were *O. surinamensis*. Mr. D. W. Hall, of the Pest Infestation Laboratory, has found *O. surinamensis* in cereals and cassava in Nigeria and the Gold Coast.

Laemophloeus has been identified to species by one of us (R. W. H.) since 1951. *L. minutus* (Ol.) has been received 43 times on cargoes from West Africa, 29 from cocoa, 7 from benniseed and 3 from Sierra Leone groundnuts, but not once from Nigerian groundnuts or from palm kernels. Of the 80 records of *L. ferrugineus* (Steph.), 49 were from groundnuts, 9 from palm kernels, 8 from cocoa, and 4 from benniseed. *L. turcicus* Grouv. was taken twice on cocoa and three unidentified species have also been found. It appears that *L. ferrugineus* is dominant in the drier areas and *L. minutus* in the damper regions, except on palm kernels.

Cotterell (1952) and Howe (1952) found *Alphitobius laevigatus* (F.) but not *A. diaperinus* (Panz.) in Nigeria. A check by the area entomologists of the Infestation Control Division has confirmed that both species occur in the shipments, and Mr. D. W. Hall collected *A. diaperinus* in Ibadan, Nigeria.

In the reports, *Carpophilus* and *Dermestes* are usually identified to species which have been grouped together in this summary. The *Dermestes* species mentioned are *D. maculatus* Deg., *D. ater* Deg., *D. frischii* Kug., *D. carnivorus* F. and *D. lardarius* L., the first being much the most common and the last probably not a West African species. Most of the *Carpophilus* were *C. dimidiatus* (F.), *C. hemipterus* (L.) or *C. obsoletus* Er., but *C. ligneus* Murray and *C. maculatus* Murray are also named.

Territories and Products.

The ships included in this survey generally trade exclusively with West Africa, very few making transit calls on journeys from more distant countries. During the war, the regularity of the run was less marked than it was subsequently. The territories considered here as West Africa extend from Angola to Senegal, but the bulk of the British imports come from the four British colonies and their mandated territories. Imports from the French colonies came to Britain during the war. There are two distinct climatic areas, the tropical forest with continuously high humidity and the savannah with a well-marked dry season. The chief exports of the former are cocoa, palm kernels, copra, coffee, dried bananas and ginger, and of the latter, groundnuts, sheanuts, benniseed, cotton seed and hides. Groundnuts may be exported in the shell or they may be decorticated first. Decortication is usual in Nigeria and the neighbouring territory of French Niger; these nuts are exported through Nigerian ports in the more humid zone. Groundnuts are not shelled in Senegal, Gambia or Portuguese Guinea, and the ports for these are in areas having a dry season. In Sierra Leone, some groundnuts are shelled and some are not.

It is usual for ships to call at a number of ports on each voyage and each ship may carry many kinds of produce, or may load the same type of goods at several ports. At each port, insects may fly on or off the ship, so it is not possible to determine if the various countries differ in infestation. In any event, this ready cross infestation on ship and between ship and port makes such differences unlikely. One trade, that in unshelled groundnuts, attracts a special fleet of tramp ships which apparently call at one port only, load only the one crop and complete the voyage in less than three weeks. Other ships take about six weeks for a voyage, except the passenger steamers which arrive two weeks after leaving Lagos, calling only at Takoradi and Freetown. These carry some general cargo.

In summarising reports, the units used are ship-voyages, each product inspected being counted, the presence or absence of each species noted, and for the more recent inspections the level of infestation also. If a ship called at more than one British port and was inspected at each, the findings at the ports are combined. The figures given refer to the month of the first inspection in Britain for the voyage, and so usually show the infestation in West Africa one month earlier. Examination on ship largely but not entirely eliminates the risk of cross-infestation in Britain before inspection here. A source of error in attributing the species found on a ship to the country of origin of the produce is cross-infestation from residues of produce from some other country left in the hold from a previous voyage. Another possible source of cross-infestation is the ship's stores.

A large proportion of the ships examined trade continuously and exclusively with West Africa. The few which make only occasional trips to this area may harbour atypical species and may even introduce them into the area. It is very likely that these unusual calls were sufficiently common during the two world wars to introduce a number of new pests of stored products into West Africa.

Insect Infestation of Produce.

General.

Although the infestation of all the crops is strikingly similar, the insects from each type of produce will be dealt with separately. There are, however, a few species which are especially associated with particular crops (Tables I and X); some, such as *Dermestes* spp. on bones, hides and copra, and *Caryedon fuscus* (Goeze) on groundnuts in shell are to be expected. Other less obvious associations are *Alphitobius* spp. with groundnuts in shell, Anthocorid bugs with dried bananas, *Araecerus fasciculatus* (Deg.) with cocoa, ginger and sheanuts, *Carpophilus* spp. with dried bananas and copra, *Corcyra cephalonica* (Stnt.) with groundnuts, whether shelled or not, *Lasioderma serricorne* with cocoa beans, soya beans and ginger, *Oryzaephilus* spp. with copra, *Plodia interpunctella* (Hb.) with groundnuts, *Tenebroides mauritanicus* (L.) with decorticated groundnuts and benniseed, *Tribolium confusum* Duv. with groundnuts in shell, and *Trogoderma granarium* with decorticated groundnuts.

The basic similarity of infestation is due to the ease of cross-infestation at so many points on the journey to the United Kingdom, especially in the holds of ships. Moreover, the insect numbers in West Africa rapidly become very large when favourable foodstuffs such as groundnuts and copra are available and the climates are such that most insects are very active at some time of day. The most abundant species on all crops, therefore, are the active, rapidly breeding forms, especially those with a catholic taste in food such as *Tribolium castaneum* (Hbst.), *Ephestia cautella* and *Necrobia rufipes* (Deg.).

In spite of this eventual similarity, certain groups of species are associated originally in the producing countries with particular crops or regions. Thus *Necrobia* is primarily found on palm kernels and copra, *Lasioderma* and *Araecerus* are associated with cocoa, and *T. castaneum*, *Trogoderma*, *Oryzaephilus*, *Corcyra* and *Plodia* are typically decorticated groundnut species. Some species are not very tolerant of low humidity and are therefore rare or absent in the drier inland northern regions of West Africa. These typical southern species include *Ahasverus advena* (Waltl), *Araecerus*, *Carpophilus*, *Lasioderma* and *Necrobia*. In the discussion that follows it is assumed that the observed intrusion of other species into these natural groupings implies cross-infestation either in West African ports where the produce is stored pending shipment or on board ship. *E. cautella* is the only important species which breeds on all the major exports in all areas.

TABLE I.

Percentage of cargoes infested by common species.

Cargo	Palm kernels	Cocoa beans	Groundnuts		
			1947–1952		1942–1946
			in shell	decorticated	both
Number of cargoes inspected	1257	665	156	539	282
Ahasverus advena	16	31	3	11	9
Alphitobius spp.	7	3	23	9	10
Anthocoridae	3	6	3	1	9
Araecerus fasciculatus	6	42	0	4	1
Carpophilus spp.	13	15	13	8	11
Caryedon fuscus	1	0·3	81	0·4	16
Corcyra cephalonica	22	13	46	43	58
Dermestes spp.	6	7	4	6	5
Ephestia cautella	79	93	57	86	94
Laemophloeus spp.	14	13	4	31	19
Lasioderma serricorne	7	59	6	3	7
Necrobia rufipes	93	48	4	49	50
Oryzaephilus spp.	35	10	28	38	37
Plodia interpunctella	7	12	8	34	32
Tenebroides mauritanicus	28	22	4	40	48
Tribolium castaneum	87	65	60	99	92
Tribolium confusum	3	2	44	3	10
Trogoderma granarium	2	1	0	28	1
No. free of insects	7	11	1	0	0

Major Export Crops.

Cocoa.

The percentage of the 665 inspected cargoes infested by the commoner insect pests is given in Table I. *Ephestia cautella* is easily the most frequent species although it does only superficial damage to cocoa beans (Cotterell, 1952). *T. castaneum*, the next in order of frequency, is not a pest of cocoa

TABLE II.

Number of inspected cargoes on which figures 1 to 7 are based.

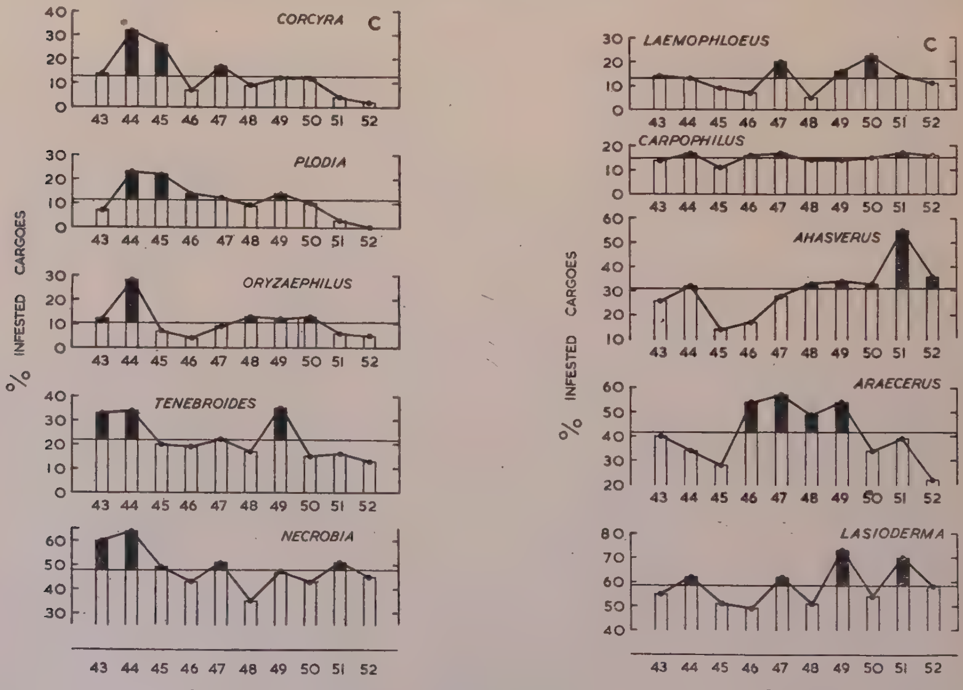
Number of cargoes year by year.

Year	'43	'44	'45	'46	'47	'48	'49	'50	'51	'52	Total
Cocoa beans ..	42	53	74	69	65	78	74	67	69	64	655
Groundnuts ..					81	97	97	115	62	87	539
Palm kernels ..	68	87	115	127	118	122	157	162	152	133	1251

Total of cargoes month by month summed for the years 1947–1952 inclusive.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Cocoa beans ..	44	46	46	53	37	28	27	30	25	23	26	32	417
Groundnuts ..	58	44	55	40	42	38	36	52	42	48	43	41	539
Palm kernels ..	69	57	70	61	62	67	65	97	79	78	79	60	844

elsewhere and does not breed on it as well as on many other foods. Its abundance is due to the transit of infested groundnuts to the same ports. *Lasioderma serricorne*, which affects nearly 60 per cent. of cargoes is the most serious pest of cocoa, since it can attack undamaged dry beans. *Araecerus fasciculatus* which can attack undamaged beans if they have a sufficiently high moisture content was the fifth most frequent species. Four of the remaining eight species which are found on more than 10 per cent. of cargoes are probably acquired from other crops, *Necrobia rufipes* from palm kernels, and *Corcyra cephalonica*, *Plodia interpunctella* and *Oryzaephilus* spp. from groundnuts. Of the others, *Ahasverus advena* is a mould feeder, *Laemophloeus minutus* suffers a high developmental mortality at low humidities, *Tenebroides mauritanicus* is partly predatory and is probably mainly acquired by spread from groundnuts, and the *Carpophilus* spp. probably feed on the dried mucilage adhering to the cocoa bean or on the odd damp bean which is starting to rot. These conclusions are based on the totals for the eleven years 1942–52; the yearly figures show some deviations, in part due to smaller numbers of cargoes on which percentage occurrence is based. Excluding 1942, when only ten cargoes were inspected, the yearly totals of cargoes inspected vary between 42 and 78 (Table II). The yearly figures for the occurrence of four of the five species likely to be acquired from groundnuts show closely similar fluctuations. These four, *Corcyra*, *Oryzaephilus*, *Plodia* and *Tenebroides*, were all comparatively frequent in 1944, and comparatively rare in 1952 (fig. 1, a). The two moths were also relatively common in 1945 and rare in 1951. The increase of these species was associated with the increasing storage period of part of the groundnut crop, which by 1946 had begun to exceed 12 months, and the decrease with the shortening of the storage period following the poor crop of 1950. The percentage occurrence on cocoa of the other



a b

Fig. 1 (a & b).—Percentages of inspected cargoes of cocoa beans infested by certain species, showing level of infestation for each year and average level for whole period.

groundnut species, *Tribolium castaneum* (fig. 7), fluctuated violently. It was comparatively frequent in 1947, 1949 and 1951, and least common in 1945 and 1952, but it is not possible to relate these changes to any known factor.

There are no very obvious explanations for the yearly fluctuations of the typical cocoa insects which are shown by figs. 1, b and 7. One species group, *Carpophilus* spp., was found almost consistently on 14 to 17 per cent. of cargoes examined, and *Ephestia* (fig. 7) infested over 90 per cent. of cargoes nearly every year. Most of the others show a marked deviation from average in at least one year but these deviations are somewhat peculiar. Thus the moisture-loving, mould-eating beetle, *Ahasverus*, was especially frequent in 1951 at the same time as *Lasioderma* which can attack and may flourish best in dry cocoa. It was scarcer than usual or about average from 1946 to 1949 when *Araecerus*, which can only breed in moist cocoa, was most frequent. In 1949, both *Araecerus* and *Lasioderma* were frequent. The whole picture may be somewhat confused by the destruction in Nigeria of some cocoa due to heavy infestation by *Lasioderma* (Hayward, 1954).

The occurrence of *Necrobia* on cocoa corresponds fairly closely with its incidence on palm kernels, the product with which it is usually associated.

The data for 417 inspections during the years 1947–52 are collected by the month of inspection (Table II) and can be used to indicate if there is a seasonal variation of insect abundance in the cocoa areas. The major part of the cocoa crop is harvested from October to December but a light crop is also harvested from May to July. The main crop can therefore begin to arrive at British ports

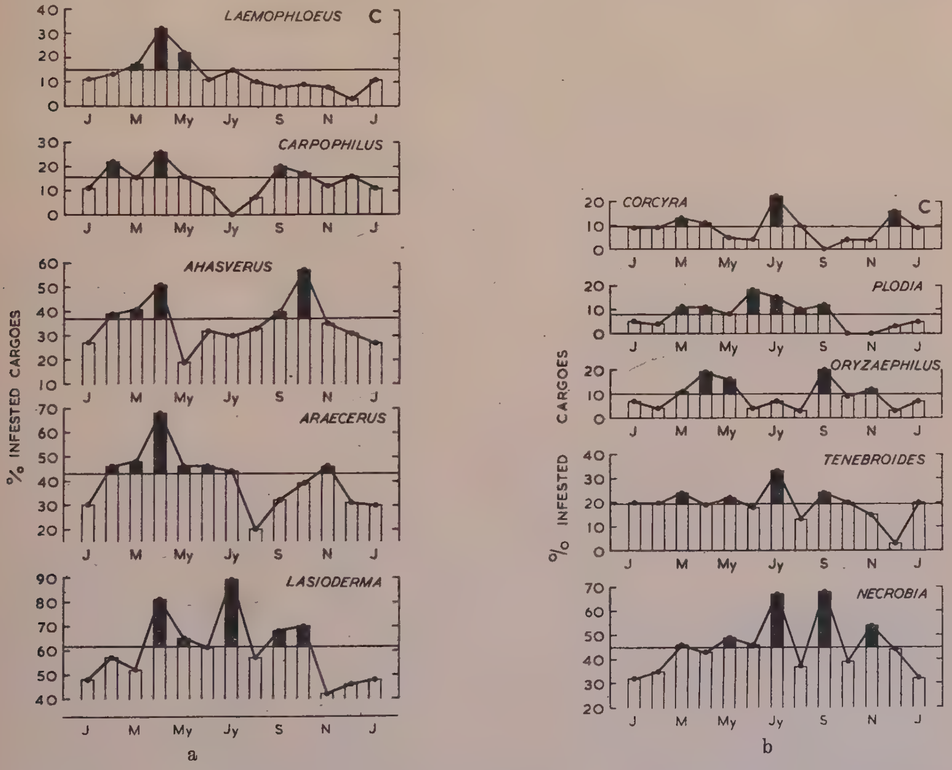


Fig. 2 (a & b).—Percentages of inspected cargoes of cocoa beans infested by certain species, showing level of infestation for each month over period 1947 to 1952 and average level for this period.

in November and the light crop in June. The main crop is usually cleared finally in June. Both the primary cocoa pests, *Araecerus* and *Lasioderma* (fig. 2, a) were least frequent when the new main crops began to arrive between November and January. Towards the end of the season, in April, these species were most abundant. During the light crop period, these species showed another increase in frequency from August to October or November. *Lasioderma* was also remarkably common in July. Except for *E. cautella* (fig. 4), most of the other species, especially *Ahasverus*, *Oryzaephilus* (fig. 2) and *T. castaneum* (fig. 4), show a similar pattern of occurrence with two periods of frequent occurrence, in April and about October, and two of comparative scarcity about December or January and August. All the species which may be acquired by cocoa, partly or entirely from the other crops, showed a more or less increased frequency in July. This shows in the data for species which were very common such as *E. cautella*, *Necrobia*, *T. castaneum* and *Tenebroides* as well as for *Corcyra* and *Plodia* which were found on less than 10 per cent. of cargoes during the period after 1947. A slight July peak shows for *Laemophloeus* (which may have included some records of *L. ferrugineus* from groundnuts) but there is none for *Ahasverus* or *Carpophilus*. This peculiarity is not ascribable to one freak year in the period. It might be attributed to especially favourable conditions for insect spread in West African ports in June, one of the most humid months, but this is discounted by the lack of a corresponding peak occurrence of insects on palm kernels and groundnuts. Most likely it is caused by the clearance in June of the remaining stocks of main crop cocoa. Apart from the July peak, *E. cautella* was slightly more frequent between December and May (94–98% of cargoes infested) and slightly less frequent between June and November (88–92%). This corresponds with observations made in southern Nigeria by Mr. J. Riley. He finds that *E. cautella* decreases in numbers after March, when *T. castaneum* is especially numerous. He also finds *Ahasverus* abundant in February and March and *Lasioderma* increasing up to June.

Discussion so far has been limited to the question of presence or absence of a species. The results of the 274 inspections over the four years 1949–52 have been analysed for the degree of infestation. In this period *T. castaneum* was placed in the "heavy" category twice but no other species was ever considered above the category "medium". Details of levels of infestation are given in Table III for species found on over ten per cent. of cargoes during this period. It is interesting to note that only *T. castaneum*, *E. cautella*, *Lasioderma* and *Ahasverus* occur more than ten times in "medium" numbers. *Araecerus* and *Necrobia* were recorded as "few" on over ten per cent. of cargoes.

TABLE III.

Infestation levels of the commoner species found on 274 cargoes of cocoa beans inspected from 1949 to 1952 inclusive.

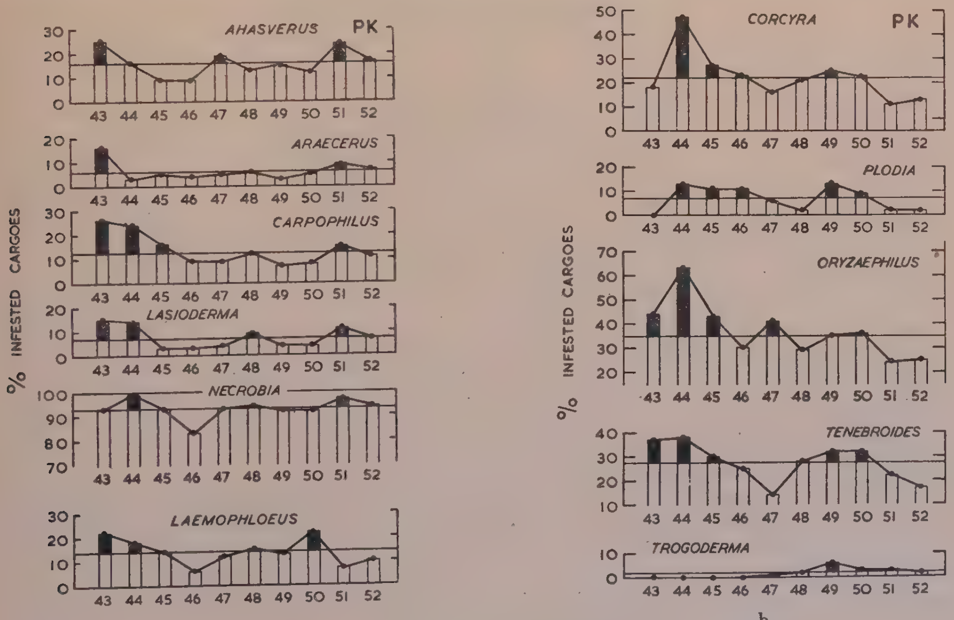
Species	Medium or heavy*	Few	Very few	Total infested
Ephestia cautella	88	94	77	259
Tribolium castaneum ..	20 (2)	57	114	191
Lasioderma serricorne ..	33	67	75	175
Necrobia rufipes	9	39	80	128
Ahasverus advena	15	35	58	108
Araecerus fasciculatus ..	7	36	61	104
Tenebroides mauritanicus ..	4	9	42	55
Laemophloeus (*minutus*) ..	5	8	31	44
Carpophilus spp.	1	11	29	41

* The number of "heavy" included in these figures is shown in brackets.

Palm kernels.

The percentage of the 1,257 inspected cargoes infested by the common insect pests are given in Table I. *Necrobia rufipes* was the species found most frequently, but *Tribolium castaneum* and *Ephestia cautella* were also found on over three quarters of the cargoes inspected. Palm kernels are very hard and resistant to damage by insects, and those species feeding on them probably live on the remains of mucilage adhering to the kernels or on broken and damaged kernels. *T. castaneum* probably feeds on the dried mucilage although its presence is mainly due to cross-infestation from groundnuts. Six other species were found on ten per cent. or more of cargoes; four of these may have spread from groundnuts. *Oryzaephilus* spp., *Tenebroides mauritanicus*, *Corcyra cephalonica* and *Laemophloeus ferrugineus*, but the other two are species preferring high humidity, *Ahasverus advena* and *Carpophilus* spp.

The yearly totals of cargoes inspected range from 68 to 162 (Table II). The yearly variations of frequency were closely similar for the five southern species, *Necrobia*, *Ahasverus*, *Araecerus*, *Carpophilus* and *Lasioderma* (fig. 3, a). Most of them were more frequent than average in 1943 and 1944, falling to their lowest levels in 1946, and after that showing small peaks in 1947 or 1948 and 1951. The species most likely acquired from groundnuts, *Corcyra*, *Plodia*, *Oryzaephilus*, *Tenebroides* (fig. 3, b) and *Laemophloeus* (probably *ferrugineus*) (fig. 3, a) also show similar variations of frequency. Most of them were relatively common from 1943 to 1945 and again in 1949–50, but relatively rarer in 1946 to 1948 and in 1951–52. *Trogoderma* (fig. 3, b), not recorded on palm kernels until 1947, had a peak abundance in 1949. The variations in these groundnut species resemble those for these species on groundnuts but the pattern of abundance of the southern species on cocoa and palm kernels is quite unrelated. There are occasional departures from the generalisations made above, as for example, the complete absence of *Plodia* in 1943 and the abundance of *Oryzaephilus* in 1947,



a b

Fig. 3 (a & b).—Percentages of inspected cargoes of palm kernels infested by certain species, showing level of infestation for each year and average level for whole period.

but these cannot be explained. Nor are there any obvious reasons for the erratic variations of the common species *T. castaneum* (fig. 7). *E. cautella* is relatively consistent in its occurrence.

Over the six years 1947–52, 844 cargoes of palm kernels were inspected, the examinations being distributed fairly evenly through the year (Table II). Monthly totals of inspections ranged from 57 in February to 97 in August. There is little evidence of a seasonal variation in insect fauna for this product which is harvested more or less continuously, but there is some indication (fig. 4) that the southern species were least frequently recorded in April and May, *i.e.*, at the end of the dry season.

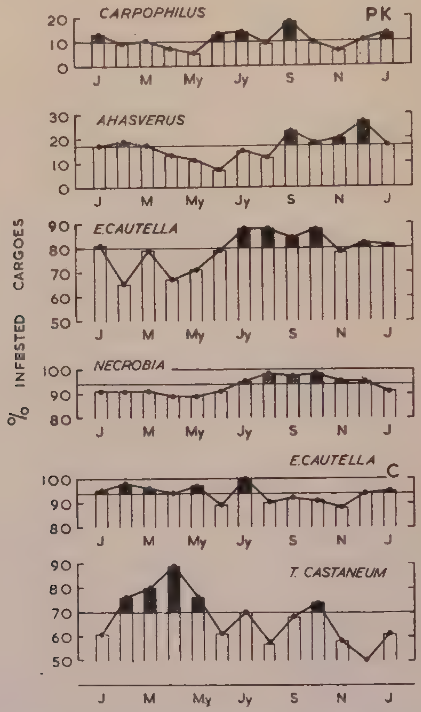


Fig. 4.—Percentages of inspected cargoes of palm kernels and cocoa beans infested by certain species, showing level of infestation for each month over period 1947 to 1952 and average level for this period.

There were 604 inspections of palm kernel cargoes over the four years 1949–52, and these have been summarised for degrees of infestation. Three species only were found as " heavy " infestations, *T. castaneum* six times and *Trogoderma* and *Ahasverus* once each. The first two species occurred as a result of cross-infestation and the latter is a mould feeder. Fuller details of the infestation levels of species found on ten per cent. of cargoes are given in Table IV. Apart from the three common species, the infestation level seldom reached the category " medium ", the fifteen records for each of *Corcyra* and *Oryzaephilus* representing only one cargo in forty.

Groundnuts in shell.

Before 1947, the summary of inspection results did not distinguish between shelled and unshelled groundnuts. The results for the later years show distinct faunistic differences between the two states of groundnut which make a detailed

TABLE IV.

Infestation levels of the commoner species found on 604 cargoes of palm kernels inspected from 1949 to 1952 inclusive.

Species	Medium or heavy*	Few	Very few	Total infested
Necrobia rufipes	186	250	130	566
Tribolium castaneum . .	146 (6)	237	155	538
Ephestia cautella	86	189	206	481
Oryzaephilus spp.	15	43	121	179
Tenebroides mauritanicus . .	5	32	127	164
Corcyra cephalonica . .	15	41	56	112
Ahasverus advena	11 (1)	48	44	103
Laemophloeus (*ferrugineus*) . .	8	21	51	80
Carpophilus spp. . .	3	13	45	61

* The number of "heavy" included in these figures are shown in brackets.

analysis of the earlier period unprofitable. Table I gives the details of infestation of groundnut cargoes for the two kinds separately since 1947, and for the two combined before that date. *Caryedon fuscus* was the species most often found in the 156 cargoes of groundnuts in shell. Seven other species were found in more than ten per cent. of cargoes, and since the opportunities for cross-infestation of this crop are slight, these must be presumed to be associated with the crop in the producing countries. These species are given in Table V.

TABLE V.

Infestation of groundnuts in shell showing number of cargoes found to harbour the commoner species between 1947 and 1952.

Year	'47	'48	'49	'50	'51	'52
No. of cargoes	25	11	26	31	26	37
Caryedon fuscus . .	18	7	22	30	21	29
Tribolium castaneum . .	11	8	25	25	11	16
Ephestia cautella . .	11	8	11	17	16	26
Corcyra cephalonica . .	15	11	14	16	7	8
Tribolium confusum . .	10	4	2	13	16	24
Oryzaephilus spp. . .	10	4	4	6	5	15
Alphitobius spp. . .	9	0	5	4	9	9
Carpophilus spp. . .	3	1	4	6	2	4

The yearly totals of inspections are small, ranging from 11 to 37, so that changes of infestation are difficult to establish. *T. confusum* was very scarce in 1949 but in 1951–52 was more common than *T. castaneum*. During 1951–52 also, *Ephestia cautella* was relatively more common and *Caryedon* slightly less so. *Corcyra* was abundant from 1947 to 1950, *Oryzaephilus* in 1947 and 1952 and *Alphitobius* in 1947 and 1951–52 (Table V).

Nearly all the inspections of this commodity were performed in the four months February to May (Table VI). Infestation with *Caryedon* increases during the season, as do the other beetles. *Ephestia*, however, reaches a peak in February and March and *Corcyra* in April, and become less common at the end of the season.

Caryedon was recorded as " heavy " on 5 inspections and *T. castaneum* once out of 145 cargoes, some of these being earlier in the year than April. Infestation levels for species found on at least ten per cent. of cargoes are given in Table VII. *Necrobia*, *Plodia* and *Tenebroides*, three species which are seldom found on groundnuts in shell were each found on one occasion at the level " medium ". These infestations were due to these cargoes being carried on ships which had called previously at other West African territories and loaded cargoes infested by these species. Two of these three instances involved groundnut cargoes inspected in August and September, which is after the usual shipping season for this cargo.

TABLE VI.

Infestation of groundnuts in shell grouped according to month of inspection.

Month	Jan.	Feb.	Mar.	Apr.	May	June	Aug.	Sept.
No. of cargoes	5	23	40	43	33	7	3	2
Caryedon fuscus	5	14	28	38	31	7	2	2
Tribolium castaneum	2	13	21	29	24	2	3	2
Ephestia cautella	4	17	31	19	10	4	2	2
Corcyra cephalonica	1	11	18	30	7	1	2	1
Tribolium confusum		4	16	27	16	5	1	
Oryzaephilus spp.		3	11	16	10	3		1
Alphitobius spp.		4	6	9	13	2		2
Carpophilus spp.		2	6	6	4	1		1

TABLE VII.

Infestation levels of commoner species found on 145 cargoes of groundnuts in shell inspected between 1947 and 1952, excluding 1948.

Species	Medium or heavy*	Few	Very few	Total infestation
Caryedon fuscus	72 (5)	27	21	120
Tribolium castaneum ..	22 (1)	41	25	88
Ephestia cautella	13	26	42	81
Tribolium confusum ..	20	36	9	65
Corcyra cephalonica ..	17	15	28	60
Oryzaephilus spp.	6	12	22	40
Alphitobius spp.	4	7	25	36
Carpophilus spp.	2	3	14	19

* The number of " heavy " included in these figures are shown in brackets.

Decorticated groundnuts.

The predominant insect of decorticated groundnuts was *Tribolium castaneum*, which was recorded on all but four of the 539 shipments inspected between 1947 and 1952. Other frequently recorded species were *Ephestia cautella*, *Necrobia rufipes*, *Corcyra cephalonica*, *Tenebroides mauritanicus*, *Oryzaephilus* spp., *Plodia interpunctella*, *Laemophloeus ferrugineus* and *Trogoderma granarium*, all of which were found on more than one out of every four cargoes. Of these only *Necrobia* is a species acquired during transit, but *Ahasverus advena*, another species infesting groundnuts by cross-infestation at port, was found on one-ninth of all cargoes (Table I).

The differences of fauna between shelled and unshelled groundnuts are thus considerable. Groundnuts in shell are more often infested by *Caryedon*, *Tribolium confusum* and *Alphitobius* spp. and decorticated groundnuts by *Tribolium castaneum*, *Ephestia*, *Tenebroides*, *Laemophloeus*, *Plodia*, *Trogoderma*, *Necrobia* and *Ahasverus*. These differences are partly due to the removal of the shell which considerably reduces the susceptibility of groundnuts to *Caryedon*, especially if the nuts are sacked, but increases the ease of attack by almost all other insects. Groundnuts in shell are not usually kept long in store before export so that only a few species are able to multiply during this period, whereas, since 1939, decorticated groundnuts have been retained in store for many months enabling large populations of the eight species mentioned above to build up on them. *T. confusum* appears (Howe, 1952) to have been reduced in Nigeria by competition with *T. castaneum*. *Necrobia* and *Ahasverus* are acquired by cross-infestation to which groundnuts in shell are less exposed. The figures for 282 inspections prior to 1947 are in fair accord with the later inspection figures, if it is assumed that numbers inspected were, as later, in the ratio of about 2 of groundnuts in shell to 7 of decorticated nuts. However, five species were evidently more abundant before 1947, the moths *Corcyra* and *Ephestia*, the beetles *Necrobia* and *Tenebroides*, and the predatory Anthocorid bugs. On the other hand *Trogoderma* was recorded only four times on groundnuts before 1947, and two of these were on nuts from Senegal.

It is noteworthy that *Necrobia* and the groundnut species, *Corcyra*, *Plodia*, *Oryzaephilus* and *Tenebroides*, were all abundant on both cocoa and palm kernels as well as on groundnuts in one or more of the years 1943–45.

Six years is rather a short period to use to give an average for infestation frequency but it has to be employed here as a gauge for comparison. Of the

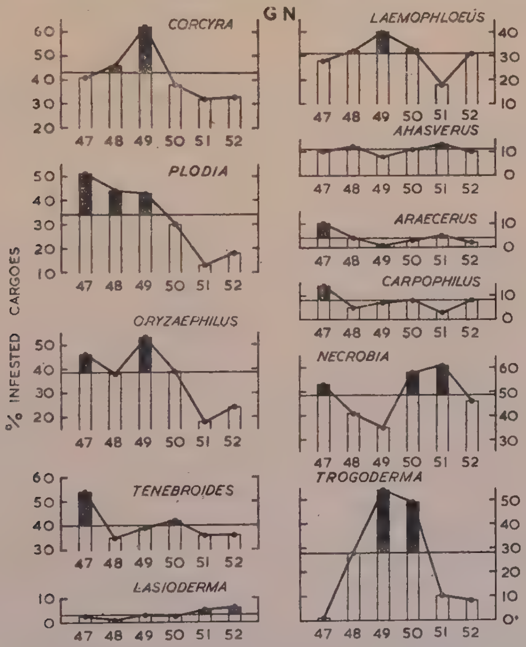
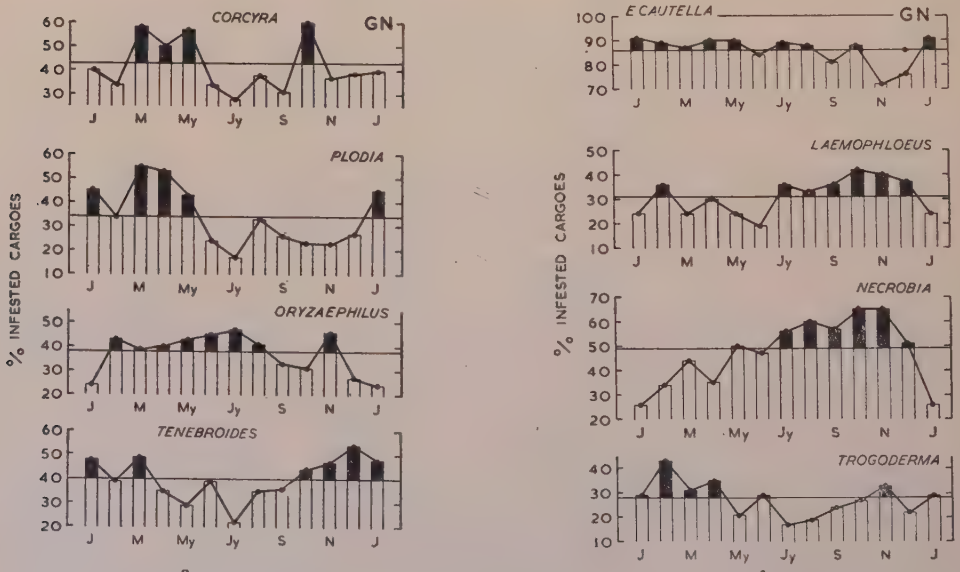


Fig. 5.—Percentages of inspected cargoes of decorticated groundnuts infested by certain species, showing level of infestation for each year and average level for whole period.

]

true groundnut species, *Ephestia* (fig. 7) and *Tenebroides* (fig. 5) were most frequent in 1947, *Plodia* in 1947–49, and *Oryzaephilus* in 1947 and 1949. *Corcyra* and *Laemophloeus* reached a peak in 1949 and in both 1949 and 1950 *Trogoderma* affected about half the cargoes. *Ephestia* was least frequent in 1949, *Plodia* from 1950 to 1952, *Oryzaephilus* and *Corcyra* in 1951 and 1952, and *Laemophloeus* in 1951 only. *Carpophilus* and *Araecerus* were more than usually frequent in 1947. *Necrobia* was most frequent in 1950 and 1951 and least frequent in 1948 and 1949 (fig. 5).

Groundnuts are marketed in November and the new crop can be expected to begin arriving in Britain in December or January. Unfortunately, for four of the six years some of the groundnut crop remained in store for well over 18 months, so that from January to June some unknown proportion of the cargoes comprised nuts under six months old and others were nuts over 12 months old. This is certain to mask both changes in insect population due to long storage and those due to season, and makes interpretation of the observed differences hard to interpret. Also, movement of groundnuts in 1949 and 1950 was to some extent determined by the degree of *Trogoderma* infestation, and since 1949, there has been a systematic campaign of control measures (Howe, Hayward & Cotterell, 1952). No consistent picture of seasonal change can be extracted from the data (fig. 6). *Plodia* was most frequent from January to May, probably corresponding to a greater frequency of this species on new crop nuts, *Corcyra* was frequent from March to May and also in October, probably occurring mostly on old nuts. *Oryzaephilus* was most frequent from February to August, *Laemophloeus* from July to December and *Tenebroides* from October to March. *Plodia* was less frequent than average from June to December, *Oryzaephilus* in December and January, *Laemophloeus* in most months between January and June, *Tenebroides* from May to July, *Corcyra* from July to September and *Ephestia* in November and December. There is perhaps some tendency to a general fall of infestation in December with the advent of the new crop. For



a

b

Fig. 6 (a & b).—Percentages of inspected cargoes of decorticated groundnuts infested by certain species, showing level of infestation for each month over period 1947 to 1952 and average level for this period.

some species, there is another fall somewhere between May and July, due to the diminishing amount of very old nuts shipped. *Necrobia* was acquired in transit most frequently from July to November and least often in January and February.

No fewer than 19 of the 361 cargoes inspected between 1949 and 1952 carried a heavy infestation of *Tribolium castaneum*. There were six records of heavy infestation of *Trogoderma* and one of *Ephestia*. About three quarters of all *Tribolium* infestations reached the category " medium ", but only *Ephestia* and *Trogoderma* of the other species were as abundant as this on many cargoes (Table VIII). The remaining five groundnut species were recorded as " medium " on from 10 to 21 cargoes, and *Necrobia* reached this level in just under one cargo in twelve. The heavier infestations were not grouped at any particular time of year for any species.

TABLE VIII.

Infestation levels of commoner species found on 361 cargoes of decorticated groundnuts inspected between 1949 and 1952.

Species	Medium or heavy*	Few	Very few	Total infestation
Tribolium castaneum . .	267 (19)	76	18	361
Ephestia cautella	93 (1)	112	100	305
Necrobia rufipes	29	72	78	179
Corcyra cephalonica . .	21	59	73	153
Tenebroides mauritanicus . .	10	40	89	139
Oryzaephilus spp.	12	45	73	130
Trogoderma granarium . .	55 (6)	35	31	121
Laemophloeus (ferrugineus) . .	13	44	58	115
Plodia interpunctella . .	12	29	60	101
Ahasverus advena	4	10	23	37

* The number of heavy included in these figures are shown in brackets.

Comparison of crop infestation.

The decorticated groundnut cargoes inspected came principally from Nigeria, the cocoa from the Gold Coast and Nigeria, and the palm kernels from Nigeria and Sierra Leone. These cargoes pass through the same ports and are carried on the same ships and the ensuing cross-infestation is shown by the close similarity of the list of infesting insects from each commodity. *Trogoderma* and *Lasioderma* are, however, largely confined to one crop. This is not surprising for *Trogoderma*, the adult of which does not fly, but the failure of *Lasioderma* to infest groundnuts is hard to explain. Probably it cannot compete with the established infestation on this crop. *Oryzaephilus* is comparatively scarce on cocoa, possibly finding it unpalatable. Some of the more striking associations of insects with a particular crop have been mentioned previously on p. 645.

The yearly fluctuations in frequency of the species on each crop are usually closely related, there seldom being more than three out of the ten years which show any marked difference in trend. Thus the species introduced mainly on groundnuts, *Corcyra*, *Plodia*, *Oryzaephilus* and *Tenebroides* (figs. 1, 3, 5 and Table IX) tended to be abundant on cocoa and palm kernels in the same years as they were abundant on groundnuts (1944) and rare on these crops when they were rare on groundnuts (1951–52). Sometimes the insects appear to have spread from groundnuts to only one of the other crops, for example, *Corcyra* was exceptionally frequent on groundnuts (Table IX) and cocoa (fig. 1) in 1945 but only a little more frequent than average on palm kernels (fig. 3) while the abundance of *Oryzaephilus* on groundnuts in 1945 and 1947 is reflected by abundance on palm kernels but not on cocoa. Occasionally abundance on groundnuts is not reflected by an increase on either of the other crops (*e.g.*, *Plodia*, 1947–48).

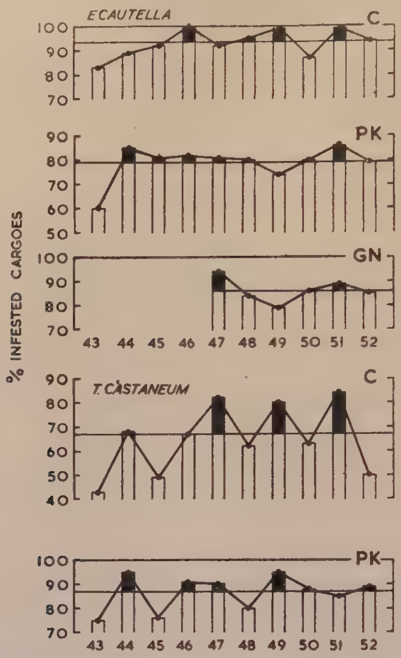


Fig. 7.—Percentages of inspected cargoes of cocoa, palm kernels and decorticated groundnuts infested by *E. cautella* and *T. castaneum*, showing level of infestation for each year and average level for whole period.

Tribolium castaneum, which was found on almost every cargo of groundnuts, was most inconsistent in its frequency on cocoa and palm kernels. *Necrobia*, which is introduced mainly on palm kernels, was found on cocoa and groundnuts more frequently than usual in 1943–44 and less frequently in 1948. In 1949 spread to groundnuts was below average. The cocoa insects, *Lasioderma* and

TABLE IX.

Percentage of cargoes of groundnuts (both in shell and decorticated) infested by certain species from 1943 to 1946.

Year	1943	1944	1945	1946	Average infestation 1947–52 for *all* groundnut cargoes
No. of cargoes inspected	17	70	70	120	
Corcyra cephalonica ..	35	67	71	49	44
Ephestia cautella ..	59	94	96	100	79
Necrobia rufipes ..	47	67	40	48	39
Oryzaephilus spp. ..	12	64	49	18	36
Plodia interpunctella ..	12	11	49	36	28
Tenebroides mauritanicus	35	46	50	49	32
Tribolium castaneum ..	82	96	93	91	90

Araecerus spread very little to the other crops. *Ahasverus* remained at a fairly steady level on groundnuts but its incidence on palm kernels and cocoa was closely similar except in 1943 and 1947. This species was infrequent on both crops in 1945–46 and common on both in 1951. *E. cautella* (fig. 7) occurs very frequently on all three crops at a fairly steady level in each. It was least abundant on all crops in 1943. Since more than one species of both *Carpophilus* and *Laemophloeus* was found, no attempt is made to correlate the occurrence of these genera on the three crops.

There is little similarity between crops of the seasonal pattern of frequency for most species. *Necrobia* is most abundant on groundnuts and palm kernels between July and December and on cocoa over a fairly similar period, a resemblance presumably due to efficient cross-infestation. *Ahasverus* and *E. cautella* are less common on palm kernels when most frequent on cocoa. None of the groundnut species show a consistent seasonal pattern but *Tenebroides* tends to be inversely related in frequency on cocoa and groundnuts.

Effects of control measures.

In 1949, groundnuts stored in Nigeria (which form the bulk of those inspected) were sprayed in an effort to reduce the population of *Tribolium*, and fumigation was introduced to combat the menace of *Trogoderma* (Howe, Hayward & Cotterell, 1952). Any attempt to elucidate the eventual success of these control measures is difficult. The 1950 groundnut harvest was poor and the 1951 harvest below average, so that with improving railment of the nuts, the extremely long storage in Nigeria, typical up to and including 1950, no longer continued in 1951 and 1952. The reduction in numbers of almost all of the groundnut insects in 1951 and 1952 reflects the combined effect of the reduced period of storage in Nigeria and the chemical control measures. The apparent reduction of *Tribolium* in Kano (Howe, Hayward & Cotterell, 1952) in 1949–50 is not reflected in the inspection figures, for this species has been found on every cargo of groundnuts inspected since April 1948, and the numbers of heavy infestations have increased. Fumigation against *Trogoderma* has been necessary each year, but the results in 1951 and 1952 were encouraging (fig. 8).

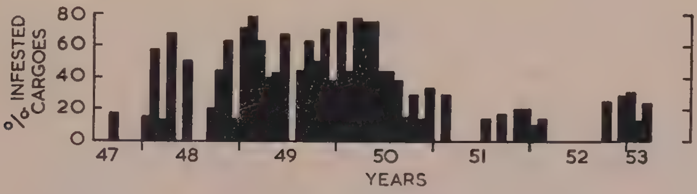


Fig. 8.—Percentages of cargoes of decorticated groundnuts found to be infested by *Trogoderma*, grouped by month of inspection. (July 1947 to March 1953.)

Other Export Crops and Produce.

Table X shows the species which were most commonly found on the less common West African exports. Some of these types of produce, notably coffee beans, beans, chillies and hides, were comparatively free of insects. *Tribolium castaneum*, *Ephestia cautella* and *Necrobia rufipes* were among the most frequent species on almost all these types of produce.

The beans were mostly grown in Nigeria and Angola, and were variously described as haricot, butter, Angola, Calabar, and feed beans. Although the beans often showed holes, Bruchids were rarely found. The species of this family recorded were *Acanthoscelides obtectus* (Say), *Callosobruchus chinensis*

TABLE X.

Infestation of various minor exports by the commoner insect species.

	Beans	Benniseed	Bones	Castor seed	Chillies	Cocoa cake	Coffee beans	Copra	Cotton seed	Dried banana	Ginger	Groundnut cake	Hides	Shea	Soya beans	Miscell.	Total no. of records
Number of Cargoes ..	26	128	11	36	10	14	76	90	109	32	28	13	22	73	20	45	733
Insect free	9	8	0	5	4	1	27	2	2	1	5	0	8	1	1	4	78
Ahasverus advena ..	1	1	—	±	—	1	1	+	1	+	1	1	—	+	1	1	81
Alphitobius spp.	1	—	1	1	—	—	1	1	1	1	—	—	—	±	—	1	25
Anthocoridae	1	1	—	—	—	—	1	1	1	±	—	1	—	1	—	1	20
Araecerus fasciculatus ..	—	1	—	1	—	1	±	1	1	—	+	—	—	+	1	1	63
Carpophilus spp. ..	—	1	—	1	—	1	—	+	1	++	1	1	—	1	—	1	90
Caryedon fuscus	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3
Corcyra cephalonica ..	1	+	—	1	—	—	1	+	+	—	1	1	1	+	1	1	112
Dermestes spp.	1	—	++++	—	1	—	—	+	1	—	—	1	++	1	1	1	57
Ephestia cautella	+	++	1	++	1	++	+	+++	++	++	+	+++	1	+++	++	+	436
Laemophloeus spp. ..	1	±	—	1	—	1	1	±	±	1	1	1	—	±	—	±	87
Lasioderma serricorne ..	+	1	—	±	1	1	1	±	±	—	+	—	—	1	+	1	79
Necrobia rufipes	±	+	++	++	+	1	+	++++	+	+	+	++	1	++	1	+	332
Oryzaephilus spp. ..	±	±	—	±	1	1	1	++	+	+	±	+	—	±	1	±	154
Plodia interpunctella ..	—	±	1	1	1	—	1	1	±	±	±	—	—	±	1	1	67
Tenebroides mauritanicus	±	+	1	+	1	1	1	±	+	±	1	+	—	+	+	+	177
Tribolium castaneum ..	++	+++	+	++	++	+++	+	+++	++++	++	++	++++	1	++++	+++	+++	551
Tribolium confusum ..	—	1	—	—	1	—	1	1	1	—	1	—	—	1	—	1	13
Trogoderma granarium	—	1	—	—	—	—	—	1	1	—	—	1	—	1	—	1	15

Species found on over 90 per cent. of cargoes examined	++++
75–90 ,, ,, ,, ,, ,, ...	+++
50–75 ,, ,, ,, ,, ,, ...	++
20–50 ,, ,, ,, ,, ,, ...	+
10–20 ,, ,, (but not less than 4 cargoes) ...	±
at least one cargo	1
absent	—

(L.), *C. maculatus* (F.) and *Zabrotes subfasciatus* (Boh.). *Lasioderma* can attack undamaged beans.

Benniseed for export is grown mainly in the southern part of the northern provinces of Nigeria but is also grown in the Gold Coast. Except for the almost complete absence of *Trogoderma*, benniseed carries the same species as groundnuts but at a lower level and frequency of infestation. It is unlikely that these small hard seeds are as susceptible to insect attack as groundnuts.

T. castaneum was only once found at the " medium " level on castor seed. No other species exceeded the level " few ".

Coffee beans were chiefly produced in the Belgian Congo and Sierra Leone, especially the former. *Araecerus*, which is commonly associated with coffee in the producing countries, was recorded 14 times.

Copra normally attracts a large and varied fauna of insects. Its flesh and the moulds growing on it are readily eaten and some of the species found breeding in copra, such as *Dermestes* spp., are partially predatory in these conditions.

Cotton seed is an export of Angola and Nigeria. It carried a varied infestation, *T. castaneum* being especially frequent. Although many of the insects found on it may have been acquired by cross-infestation, they may well have been breeding in the cotton seed, possibly on damaged seeds.

Dried bananas are produced in the Cameroons and were usually infested by all the likely dried fruit species, except *Plodia* for which there were only four records.

Ginger is an export of Sierra Leone which is typically attacked there by *Araecerus* and *Lasioderma*.

Cocoa, groundnuts and palm kernels have all been used in West Africa for expression of oil or fat and a small quantity of cake from each has been exported from Nigeria and the Gambia since 1949.

Bones and hides are typically attacked by *Dermestes* spp. and bones also by *Necrobia* spp. The commonest species of *Dermestes* is *D. maculatus* which often spreads to other produce, but *D. ater*, *D. carnivorus* and *D. frischii* have been recorded several times. Three other Dermestids, *Attagenus gloriosae* (F.), *A. megatoma* (F.) and *Anthrenus vorax* Waterh. have been recorded. *N. ruficollis* (F.) was found once on bones in addition to the more usual *N. rufipes*. The species which probably cannot breed on these goods but which have been recorded on them are *T. castaneum*, *E. cautella*, *Corcyra*, *Plodia*, and *Alphitobius diaperinus* as well as *Tenebroides* which can be predatory.

Twenty-three other different kinds of produce were seen less than ten times

TABLE XI.

Infestation level of the commoner species found on 339 cargoes of minor exports between 1949 and 1952.

Species	Medium or heavy	Few	Very few	Total	Total 1942–1952
T. castaneum	66	131	101	298	551
E. cautella	21	87	111	219	436
Necrobia	22	65	61	148	332
Tenebroides	9	17	61	87	177
Corcyra	5	22	27	54	112
Oryzaephilus	5	18	29	52	154
Laemophloeus	3	16	30	49	87
Ahasverus	7	9	23	39	81
Carpophilus	3	13	20	36	90
Lasioderma	3	8	21	32	79
Araecerus	3	14	15	32	63

each, giving 45 cargoes in all. Only *T. castaneum*, *E. cautella*, and *Necrobia* were often found on these.

Thirteen species were recorded more than 50 times on the 733 cargoes of minor exports inspected. Of these only *Plodia* and *Laemophloeus* were found on fewer than 20 per cent. of cargoes inspected for every kind of produce listed.

Over the period 1949–52, 339 cargoes of these minor exports were examined. Table XI summarises the infestation levels for the eleven species found most often. Nine other species were recorded at the level "medium", and two, *Trogoderma* and *Calandra oryzae* (L.) were recorded at the "heavy" level. *C. oryzae*, *Ahasverus* and *Lasioderma* were found at this level on Belgian Congo maize, copra and ginger, respectively. Heavy infestations of *Trogoderma* were found on benniseed, copra and cotton seed and of *T. castaneum* on benniseed, copra, cotton seed, groundnut cake and palm kernel cake.

Less Common Species and Strays.

The storage insects found on fewer than 100 cargoes are listed in Table XII.

This list is grouped according to the number of times each species was found, and includes an estimate of the abundance of each species in West Africa. These estimates are based on the papers consulted and on the observations of D. W. Hall, Colonial Liaison Officer of the Pest Infestation Laboratory in West Africa as well as on the experience of one of us (R. W. H.) in Nigeria.

TABLE XII.

A list of storage species found on the 3,632 cargoes inspected, in approximate order of frequency and with an estimate of their abundance in West Africa.

A. Species found on over 2,000 cargoes			
Ephestia cautella (Wlk.)	a	*Tribolium castaneum* (Hbst.)	a
Necrobia rufipes (Deg.)	a *		
B. Species found on over 500 cargoes			
Ahasverus advena (Waltl)	b *	*Oryzaephilus mercator* (Fauv.)	b
Corcyra cephalonica (Stnt.)	b	*Plodia interpunctella* (Hb.)	a
Lasioderma serricorne (F.)	a	*Tenebroides mauritanicus* (L.)	c
C. Species found on over 100 cargoes			
Alphitobius diaperinus (Panz.)	b	*Caryedon fuscus* (Goeze)	a
Alphitobius laevigatus (F.)	b	*Laemophloeus ferrugineus* (Steph.)	b
Araecerus fasciculatus (Deg.)	a *	*Laemophloeus minutus* (Ol.)	b *
Carpophilus dimidiatus (F.)	b *	*Tribolium confusum* Duv.	b
Carpophilus hemipterus (L.)	b *	*Trogoderma granarium* Everts	a
D. Species found on over 50 cargoes			
Dermestes ater Deg.	a *	*Lyctocoris campestris* (F.)	b *
Dermestes maculatus Deg.	a	*Xylocoris flavipes* Reut.	b *
E. Species found on over 20 cargoes			
Anthocoridae (unnamed)	b *	*Necrobia ruficollis* (F.)	?
Calandra granaria (L.)	–	*Oryzaephilus surinamensis* (L.)	b
Calandra oryzae (L.)	a	*Rhizopertha dominica* (F.)	a
Carpophilus obsoletus Er.	b *	*Sitotroga cerealella* (Ol.)	a
Carpophilus sp.	?	*Thaneroclerus buqueti* (Lef.)	c *
Cryptophagus sp.	?		

a	obvious on produce
b	numerous but unevenly distributed
c	widespread but in small numbers
d	rare
*	absent in dry conditions
–	probably unable to live in W. Africa
?	no records of occurrence known to us
(?)	no real evidence of abundance but known to occur.

TABLE XII—*continued.*

F. Species found on over 10 cargoes

Anthicus floralis (L.)	c
Attagenus gloriosae (F.)	c
Cathartus quadricollis (Guér.)	b
Dermestes carnivorus F.	c *
Dermestes frischii Kug.	c
Dermestes sp.	c
Latheticus oryzae Waterh.	d
Lophocateres pusillus (Klug)	d
Typhaea stercorea (L.)	?

G. Species found on less than 10 cargoes

Acanthoscelides obtectus (Say)	d (?)
Alphitophagus bifasciatus (Say)	–
Anthrenus vorax Waterh.	d
Aphanus sordidus (F.)	b
Attagenus megatoma (F.)	?
Bitoma sp.	?
Brachypeplus sp.	?
Callosobruchus chinensis (L.)	?
Callosobruchus maculatus (F.)	b
Carcinops quattuordecimstriata (Steph.)	c
Carpophilus ligneus Murray	?
Carpophilus maculatus Murray	?
Coccotrypes sp.	d (?)
Coninomus constrictus Gylh.	?
Corynetes analis Klug	?
Cryptophagus cellaris (Scop.)	d (?)
Dermestes lardarius L.	–
Dinoderus bifoveolatus Woll.	?
Dinoderus minutus (F.)	b (?)
Dinoderus sp.	b
Diocalandra impressicollis (Quedenf.)	d (?)
Endrosis sarcitrella (L.)	–
Enicmus minutus (L.)	?
Ephestia kuehniella Zell.	–
Gibbium psylloides (Czenp.)	d *
Gnathocerus cornutus (F.)	–
Gnathocerus maxillosus (F.)	d (?)
Gonocephalum prolixum (Er.)	?
Heterobostrychus brunneus (Murray)	c
Hofmannophila pseudospretella (Stnt.)	–
Hypophloeus sp.	?
Laemophloeus turcicus Grouv.	?
Laemophloeus sp.	d
Laemotmetus rhizophagoides (Wlk.)	?
Leurostenus filum Mshl.	d
Lyphia depressa Hint.	?
Mezium affine Boield.	–
Metophthalmus sp.	?
Monanus concinnulus (Wlk.)	?
Murmidius segregatus Waterh.	?
Mussidia nigrivenella Rag.	c *
Mycetaea hirta (Marsh.)	?
Mycetophagus sp.	?
Necrobia violacea (L.)	?
Orphinus fulvipes (Guér.)	?
Palorus ratzeburgi (Wissm.)	b
Palorus subdepressus (Woll.)	d
Palorus sp.	b
Pentarthrum cylindricum Woll.	?
Pentarthrum sp.	?
Plochionus pallens (F.)	?
Pyralis farinalis (L.)	–
Reduvius sp.	c (?)
Silvanus unidentatus (Ol.)	?
Sinoxylon anale Lesne	?
Tenebrio guineense Imhoff	c
Tenebrio molitor L.	–
Thorictodes heydeni (Rttr.)	b
Tinea columbariella Wocke	–
Tinea granella (L.)	?
Tinea pellionella (L.)	–
Tineola bisselliella (Humm.)	–
Tribolium anaphe Hint.	d
Tribolium destructor Uytt.	–
Zabrotes subfasciatus (Boh.)	d (?)

H. Species recorded but probably mostly misidentifications

Ephestia elutella (Hb.)	–
Stegobium paniceum (L.)	–
Trogoderma versicolor (Creutz.)	?

Some of the species, as for example, *Calandra oryzae*, *Sitotroga cerealella* (Ol.) and *Rhizopertha dominica* (F.) are very common in West Africa but are rare in cargoes because they are not pests of the common exported commodities. Other species, such as *Attagenus gloriosae*, are widespread on particular commodities but are easily killed or dispersed by the handling of produce. The list also contains a number of species, which, to our knowledge, have not been recorded in West Africa. These are split into two groups, one, marked –, comprising species which we would judge from knowledge of their biology to be incapable of living anywhere in the tropics, and the other, marked ?, of species which probably could live there. The first group includes residual infestation left in the holds after the removal of cargo from earlier voyages, invaders from ships' stores and strays flying on to the ship at the port of inspection in Britain. Omitted from the lists are the cockroaches, crickets and earwigs which are fairly common in the holds of ships. The commonest cockroach, *Blattella germanica* (L.), was recorded on about 100 ships. Others recorded were *Blatta orientalis* (L.), *Periplaneta americana* (L.), *P. australasiae* (F.) and *Dorylaea rhombifolia* (Stoll). Both the species of cricket recorded, *Acheta domestica* (L.) and *Gryllodes sigillatus* (Wlk.)

are known from West Africa (Corby, 1947). There were almost 50 records for earwigs including *Prolabia arachidis* (Yersin), *Anisolabis annulipes* (Lucas), and also *Forficula auricularia* L.; about sixty records of the firebrat *Thermobia domestica* (Pack.) and twenty of the silverfish *Lepisma saccharina* L. Unnamed Psocids were found thirty times and Pharaoh's ant, *Monomorium pharaonis* (L.) twice. *Bracon hebetor* Say was by far the most common parasite named. Others recorded were *Anisopteromalus calandrae* (How.), *Holepyris hawaiiensis* (Ashm.), *Plastanoxus munroi* Richards, *P. westwoodi* (Kieff.), *Nemeritis canescens* (Grav.) and *Heterospilus* sp.

Many of the ships carry timber so that timber beetles have been recorded as strays on the other cargoes or on the dunnage. These timber beetles other than those species which are sometimes associated with stored products are omitted from Table XII.

Conclusions.

The species commonly found on the 3,632 cargoes correspond closely with those now found on these products in the country of origin, but also include a few extra species acquired at the West African ports. All the species which are important on export produce in West Africa are imported with these crops into Britain. A large proportion of these are species which have been introduced into West Africa, most of them from Asia. Storage species are readily carried about the world—and most of them can attack a wide variety of foods. In general, therefore, it is the climatic factors which determine whether a storage species is to be found in any country, and the relative importance of the species depends largely on the outcome of competition between them. West Africa provides a wide range of susceptible produce and climatic conditions to suit the rapid multiplication and spread of all tropical species, but is too hot for temperate species. The spread of introduced species inland is determined mainly by their tolerance of low humidity. It seems very likely that all the major tropical storage pests, and most of the minor ones, do now occur in West Africa and that future changes in the status of pests will be determined by changes of storage policy and methods of handling, or by the introduction of control measures upsetting the present balance.

Among the important species, the one which has most recently become a serious pest is *Trogoderma granarium*. This was not recorded from Nigeria until December 1948 (Howe, 1952), and was first abundantly recorded in imported cargoes in Britain earlier that year. The first record on imported groundnut cargoes from West Africa was made in January 1943 in a ship from Senegal. The first record from Nigerian groundnuts was made in June 1943. In 1952, it was found in barley and wheat bran returned to Britain after being imported into the Gambia. Risbec & Mallamaire (1949) list *T. granarium* from stored rice in the Niger Valley area of French West Africa but state it does little damage. Hinton (1945, p. 389) records India, Ceylon, and Malaya as the original home of this species but Howe (1952) tentatively accepted that it could be native to Nigeria. It is extremely difficult to form a reliable opinion for a species such as this, which is so difficult to find when present in small numbers. Evidently, whether introduced or not, it had been present undetected for many years. If introduced it may have been imported on new or second-hand jute bags from India. This species was first introduced into Britain in barley from Karachi (Walker, 1917).

The major pest of groundnuts in shell, *Caryedon fuscus*, is certainly introduced. The spread in West Africa of a beetle which is presumably this species is discussed by de Jonghe d' Ardoye (1935). The commonest pest of shelled groundnuts, *Tribolium castaneum*, is also introduced. In Senegal, this species and *T. confusum* were both recorded on groundnuts in shell in 1916 by Roubaud and they are still about equally common on this product. In Nigeria, however, the species recorded in 1914 by Lamborn was *T. confusum*, but this species was not included in the list of pest species of Nigeria by Golding (1946). Howe (1952) suggests that *T. castaneum* may gradually be eliminating *T. confusum* in Nigeria.

The major beetle pest of cocoa, *Lasioderma serricorne*, which also seriously damages tobacco, ginger, cassava and cowpeas in West Africa, was probably introduced on tobacco. It is first mentioned in a British colony by Hargreaves (1926) in Sierra Leone, but the Review of Applied Entomology, Ser. A, vol. 9, p. 516, interprets as *Lasioderma* a pest of stored tobacco in the Cameroons mentioned by Thillard (1921).

E. cautella is probably native and was recorded by Lamborn (1914). The temperate species *E. elutella* has been recorded for the Gold Coast (Waters, 1933) but this is probably a misidentification.

Among the less important species there are a number which are slightly more or less important on cargoes than in the country of origin. Species which are relatively commoner in Nigeria than on the imported cargoes are *Anthicus floralis*, *Attagenus gloriosae*, *Palorus* spp., *Thorictodes heydeni*, *Aphanus sordidus* and the Anthocorid bugs. With the more abundant species, *Oryzaephilus* spp. and *Corcyra* are relatively over-represented on cargoes and *Laemophloeus* and *Plodia* less frequently found on cargoes than would be expected from their abundance in Nigeria.

Summary.

An analysis is made of the records of inspections for infestation by insects of cargoes imported into Britain from West Africa. The exporting territories extend from Angola to Senegal but the bulk of cargoes were produce of the four British colonies.

The ready spread of insects from one cargo to another causes infestation to be similar for all cargoes but a few species are especially associated with a particular crop. Groundnuts in shell are normally shipped alone and therefore relatively protected from cross-infestation.

The three major cargoes are cocoa, palm kernels and groundnuts which form four-fifths of the inspected shipments. Fifteen other kinds of produce are also considered.

Twelve species were found on more than ten per cent. of cargoes of cocoa beans. Of these five were probably acquired from groundnuts and one from palm kernels by cross-infestation. *Ephestia cautella* (Wlk.), *Tribolium castaneum* (Hbst.) (from groundnuts), *Lasioderma serricorne* (F.), *Necrobia rufipes* (Deg.) (from palm kernels) and *Araecerus fasciculatus* (Deg.) all infested over 40 per cent. of cargoes.

The fluctuations of infestation year by year are examined, and it is shown that these are similar for all the species acquired from groundnuts except *T. castaneum*. Variations in frequency of other species appear to be unrelated.

The data are also collected according to month of inspection. Nearly all species including both *Araecerus* and *Lasioderma* but excepting *E. cautella* were scarcest toward the beginning of both the main crop (December) and light crop (May) seasons and commonest at the end of each. *Lasioderma* and all the species acquired by cross-infestation also showed a July peak of infestation which cannot be explained with any certainty.

Nine species, five of them mainly acquired from groundnuts, were found on more than ten per cent. of cargoes of palm kernels. *N. rufipes*, *T. castaneum* and *E. cautella* infested over 75 per cent. of cargoes and *Oryzaephilus* spp. infested 35 per cent.

The yearly fluctuations were similar for the five species typical of the humid zone but those for the species acquired from groundnuts were less consistent. There was little evidence of a seasonal variation of numbers for this cargo.

Ten species infested over ten per cent. of cargoes of decorticated groundnuts but only two of these were acquired in transit through the humid ports. All but one infested over one-quarter of cargoes and *T. castaneum* was found on nearly every cargo.

Yearly variations in frequency of the eight groundnut species were fairly similar but seasonal variation was masked by the effects of the overlapping of storage periods of successive crops.

Groundnuts were much more heavily infested than the other two crops. *T. castaneum* was almost always found at the levels described here as " medium " and " heavy ".

Eight species were found on ten per cent. or more of cargoes of groundnuts in shell. *Caryedon fuscus* (Goeze), *T. castaneum*, *E. cautella*, *Corcyra cephalonica* (Stnt.) and *Tribolium confusum* Duv. infested over 40 per cent. of cargoes. Beetles increased in abundance towards the end of the season (May) but moths were most frequent in mid-season (March–April).

The infestations of each crop and the yearly and seasonal variation for each is compared.

The species commonly found on the less usual imports are listed, as also are some species often found in the dunnage of ships' holds. A list is given of all the storage species found on West African cargoes.

Acknowledgements.

This paper is a summary of a small fraction of the considerable amount of detailed work carried out by inspectors of the Infestation Control Division of the Ministry of Agriculture, Fisheries & Food. Identifications of insects were done first by the inspectors who, when in doubt, passed them to the appropriate authority for their area. These include Mrs. M. T. Armstrong, Miss E. M. Debenham, Mr. J. D. Norris and Miss G. C. Williams. Some specimens were passed on to the Headquarters entomologist, Mr. G. A. Brett.

Specialists at the British Museum and elsewhere, of whom we should mention Mr. J. Balfour-Browne and Dr. H. E. Hinton, have named many of the species. Messrs. L. A. W. Hayward and J. Riley of the West African Stored Products Research Unit have kindly allowed us to refer to their unpublished observations. The figures were drawn by Miss J. E. Currie and photographed by Mr. J. H. Hammond.

We acknowledge, gratefully, the assistance of all the above. This analysis has formed part of the programme of work of the Pest Infestation Laboratory and is published by permission of the Department of Scientific and Industrial Research and Ministry of Agriculture, Fisheries and Food.

References.

Corby, H. D. L. (1947). *Aphanus* (Hem., Lygaeidae) in stored ground-nuts.—Bull. ent. Res., **37,** pp. 609–617.

Cotterell, G. S. (1952). The insects associated with export produce in Southern Nigeria.—Bull. ent. Res., **43,** pp. 145–152.

Freeman, J. A. (1948*a*). World foci of infestation and principal channels of dissemination to other points, with suggestions for detection and standards of inspection. *In* Easter, S.S. Ed. Preservation of grains in storage.—F.A.O. agric. Stud., no. 2, pp. 15–34.

Freeman, J. A. (1948*b*). Stored-products pests: a survey of the principal entomological problems in the United Kingdom.—Ann. appl. Biol., **35,** pp. 294–301.

Golding, F. D. (1946). The insect pests of Nigerian crops and stock.—Spec. Bull. agric. Dep. Nigeria, no. 4, 48 pp.

Hargreaves, E. (1926). Report of the Entomological Section.—Rep. Dep. Lds For. S. Leone, 1925, pp. 16–18.

Hayward, L. A. W. (1954). The origins of infestations of cocoa by Tobacco Beetle in Nigeria.—Emp. J. exp. Agric., **22**, pp. 133–137.

Hinton, H. E. (1945). A monograph of the beetles associated with stored products. Volume I.—443 pp. London, Brit. Mus. (Nat. Hist.).

Howe, R. W. (1952). Entomological problems of food storage in Northern Nigeria.—Bull. ent. Res., **43**, pp. 111–144.

Howe, R. W. (1953). *Oryzaephilus mercator* (Fauv.) (Col., Cucujidae), a valid species.—Ent. mon. Mag., **89**, p. 96.

Howe, R. W., Hayward, L. A. W. & Cotterell, G. S. (1952). Control measures in 1948–50 against insects attacking groundnuts stored at Kano, Northern Nigeria.—Bull. ent. Res., **43**, pp. 259–279.

de Jonghe d'Ardoye, E. (1935). Note sur la bruche de l'arachide *Pachymoerus acaciae* Gill.—Bull. Ann. Soc. Ent. Belg., **75**, pp. 421–422.

Lamborn, W. A. (1914). The agricultural pests of the Southern Provinces, Nigeria.—Bull. ent. Res., **5**, pp. 197–214.

Risbec, J. & Mallamaire, A. (1949). Les animaux prédateurs et les insectes parasites des riz cultivés en Afrique occidentale.—Agron. trop., Nogent, **4**, pp. 70–76.

Roubaud, E. (1916). Les insectes et la dégénérescence des arachides au Sénégal.—Annu. Com. Afr. occ., 1916, pp. 363–436.

Thillard, R. (1921). La culture du tabac de Sumatra au Cameroun.—Agron. colon., **6**, pp. 23–40. (Rev. appl. Ent., (A) **9**, p. 516.)

Walker, J. J. (1917). Note on *Trogoderma khapra*, Arrow, a recently described Dermestid granary pest.—Ent. mon. Mag., **53**, p. 165.

Waters, H. B. (1933). Experimental work.—Rep. Dep. Agric. Gold Cst., 1932–33, pp. 12–16.

Appendix.

The reports of the inspections during 1953 of cargoes of produce imported from the Gambia, Sierra Leone, Gold Coast, Togo and Nigeria have recently been analysed by the Infestation Control Division and have been made available by Mr. G. A. Brett. This analysis shows that, in general, the frequency of occurrence of all species is static or decreasing.

The cargoes inspected were 214 of palm kernels, 85 of cocoa, 135 of decorticated groundnuts, 28 of groundnuts in shell and 144 of other products. All the groundnuts in shell were from the Gambia. Of the remaining cargoes, 159 palm kernels, 65 cocoa, 127 groundnuts and 108 other cargoes, respectively, were from Nigeria. This great preponderance of Nigerian produce precludes any useful comparison of the insects associated with the cargoes from each country, but the proportion infested by each species for each territory is extremely uniform. The only suggested differences between territories is that *Lasioderma* appears to be commoner on cocoa in Nigeria than in the Gold Coast whereas the reverse appears to be true for *Araecerus*.

The proportions of each of the three major commodities infested by *T. castaneum*, *E. cautella* and *Necrobia* in 1953 were very similar to the 1952 levels except that *Necrobia* was more frequent on groundnuts in 1953. The only other species to increase in frequency in 1953 was *Trogoderma* on groundnuts which was found on 21 per cent. of cargoes as against eight per cent. in 1952. Of the species typically associated with groundnuts, *Corcyra* and *Plodia* were absent from cocoa and unusual on palm kernels in 1953, and *Oryzaephilus* was found once only on cocoa. In 1953, *Oryzaephilus* was only a little less frequent and *Tenebroides* slightly more frequent on palm kernels than in 1952. Thus the trends for these species exhibited since 1949 continued in 1953.

The proportions of cargoes of Gambian groundnuts infested by each species in 1953 were close to the averages for the previous six years. Among the miscellaneous commodities, 11 out of 19 cargoes of coffee beans were insect free.

The level of infestation for every species in all commodities fell off in 1953. Even *T. castaneum* on groundnuts reached the level " heavy " only once, and the level " medium " in just over half the cargoes inspected. It was not found at all on four cargoes of decorticated groundnuts. Compared with the previous four years, the degree of infestation of cargoes by *E. cautella*, *T. castaneum*, *Necrobia* and *Lasioderma* all fell considerably. *Trogoderma* reached the level " medium " in seven per cent. of cargoes of decorticated groundnuts as compared with 14 per cent. over the previous four years.

SYSTEMIC INSECTICIDES FOR THE CONTROL OF INSECTS TRANSMITTING SWOLLEN-SHOOT VIRUS DISEASE OF CACAO IN THE GOLD COAST.

E. M.

By A. D. Hanna, E. Judenko and W. Heatherington
Chesterford Park Research Station, Essex.

(Plates XX & XXI.)

Contents.

PAGE
Introduction ... 669
Assessment of Mealybug Populations ... 671
Systemic Insecticides used ... 674
Spraying Experiments ... 674
Soil Treatment with Systemic Insecticides: Laboratory and Insectary Experiments ... 675
  Technique ... 675
  Preliminary experiments ... 676
  Persistence of insecticidal action of dimefox within seedling plants ... 679
  Phytotoxicity ... 680
  The fate of dead mealybugs ... 680
Soil Treatment with Systemic Insecticides: Field Experiments ... 682
  Technique of application of systemic insecticides to the soil ... 682
  Investigations with various insecticides ... 682
  Development of the soil treatment with dimefox ... 683
  Factors that might affect control ... 696
  Effect of control measures on beneficial insects ... 699
  Toxicity considerations ... 700
Trunk Implantation Experiments ... 701
  General experiments ... 701
  Translocation in the trunk implantation method ... 704
  Increasing the efficiency of the trunk implantation method ... 704
Conclusions ... 707
Summary ... 707
Acknowledgements ... 709
References ... 709

Introduction.

Cacao, *Theobroma cacao*, was introduced to the Gold Coast from Fernando Po some seventy years ago, and the industry has since grown to such an extent that over a third of the world's cocoa supply today is produced by the Gold Coast. The value of the 1950 crop was estimated at £54 million, which constituted over 70 per cent. of the value of Gold Coast exports.

For many years the cacao trees in the Gold Coast were apparently not seriously attacked by pests or diseases. About 1936, a condition described as dieback was recorded in the Eastern Province. Different theories were advanced to explain the cause of the unhealthy condition, such as physiological drought, nutritional deficiency and climatic conditions. It was not until 1939 that Posnette was able to show that the disease could be transmitted by grafting, and further work established that it was a virus disease, which was named swollen-shoot. Since then, the disease has caused considerable concern.

Posnette (1941) commenced investigations on the vectors of the disease, and his work was continued by Cotterell (1943). Two species of heteropterous insects, 15 species belonging to eight families of Homoptera, and the thrips, *Selenothrips rubrocinctus* (Giard), were tested. The transmission of the disease was successful in the case of the mealybugs, *Pseudococcus njalensis* Laing and *Ferrisia virgata* (Ckll.), and apparently with the Psyllid, *Mesohomotoma tessmanni* (Aulm.) and the Aphid, *Toxoptera coffeae* (Nietn.). Box (1945) carried out a number of transmission tests with Aphids, Psyllids, mealybugs including a third species, *Pseudococcus citri* (Risso), and the thrips, *S. rubrocinctus*. He obtained transmission only with the three species of mealybugs and this was confirmed by Posnette and Strickland (1948).

Strickland (1947), found that *P. njalensis* is by far the most important species of Pseudococcid on cacao in the Gold Coast, followed by *P. citri*; *F. virgata* is rare on cacao. The percentages of these three species amongst collections from nearly 3,000 trees selected at random were 98·99, 0·99 and 0·02 respectively. *P. njalensis* seems, therefore, to be the most important vector of the viruses of swollen-shoot disease in the Gold Coast. In future references in this paper to mealybugs, all the three species mentioned above will be collectively included.

There are about 500 million cacao trees in the Gold Coast, and the latest figures show that swollen-shoot has spread at the rate of 18 million trees a year since 1947. As a remedial measure, about 6,795,755 diseased trees had been cut out up to the end of September 1949, and the numbers of trees cut out in 1951, 1952 and up to August 1953 were 2,221,046, 3,982,264 and 4,624,796, respectively (Broatch, 1953).

From this short summary, it would appear that a good control of mealybugs would reduce or arrest the spread of the disease. The present method of control by cutting out visibly infected trees, involves cutting down trees before they cease to bear, and the necessity for this is not always appreciated by cacao farmers. A successful control of mealybugs would increase the efficiency of the cutting-out campaign by confining the disease to visibly infected trees, and those infected but symptomless. If, after the initial cutting-out of the trees visibly infected by swollen-shoot, the mealybug population were kept under control, by repeated applications of the control measure, until all the trees with latent infection had shown symptoms of the disease and had been cut out, the spread of the disease would, in theory, be arrested.

The report of the Commission of Enquiry into the swollen-shoot disease of cacao in the Gold Coast (Berkeley, Carter & van Slogteren, 1948), drew attention to the need for immediate investigations on the protection of cacao from the disease. One of the commissioners urged that the help of chemical manufacturers should be sought without delay. This led to an invitation to the Association of British Chemical Manufacturers to send representatives to the Gold Coast, with the support of the Colonial Office. The mission of seven scientists, including four representatives of British Chemical Industries, arrived at Accra in February 1949. Its members studied the problem on the spot, and one of their many recommendations was to try systemic insecticides for the control of the mealybugs transmitting the virus disease, on the grounds that the successful control of these vectors would increase the efficiency of the cutting-out campaign. In their opinion the discovery of a chemical means of control of the mealybugs would be one of paramount importance.

The authors of the present paper constituted the team of three scientists that was consequently appointed to work under the general administrative direction of the Director of the West African Cacao Research Institute at Tafo, in the Gold Coast, on an investigation of the possible use of systemic insecticides for the control of the spread of the swollen-shoot disease in cacao in West Africa.

This team began work at Tafo in April 1950 and, by agreement with the West African Cacao Research Institute, the initial experiments were made by the team working independently. Where these were successful, confirmatory experiments on a larger scale were then carried out jointly with the Institute. Attention is drawn in the paper to the cases in which this procedure was followed.

Pseudococcus njalensis is almost always attended by ants of the genus *Crematogaster*, which build carton tents (Pl. XX, figs. 1, 2 and Pl. XXI, fig. 1) of mainly vegetable origin over the mealybug colonies, apparently to protect them. In return, the ants feed on the honeydew secretion; if this is not removed, it becomes a medium for the growth of fungi and bacteria which eventually kill the mealybugs.

The control of mealybugs in different parts of the world is usually carried out either directly, by a contact insecticide, or indirectly, by controlling their attendant ants. The latter method was investigated by the authors but will be dealt with in a separate publication.

The protection afforded to the cacao mealybugs by their tents renders their control by contact insecticides a very difficult problem. A greater chance of success seemed possible by the use of systemic insecticides, which, when applied to any part of a plant, are absorbed and then translocated in the sap stream, rendering the whole plant toxic to sucking insects. This present work was an attempt to control the known vectors of the swollen-shoot virus, without rendering the cacao beans toxic, interfering with the known mealybug parasites and predators, or affecting the main pollinating insects. It was also an attempt to evolve a method of application that avoided as much as possible the use of heavy and elaborate machinery, which is not suitable for use amongst cacao grown under Gold Coast conditions. Cacao is grown there at an average of 600 trees per acre, without regular spacing or definite rows and these conditions, together with the fallen giant forest trees, stumps, ditches and streams that are usually found in cacao farms, do not allow the use of tractors and spraying machines.

Assessment of Mealybug Populations.

Strickland (1951) found a wide variability in the population of *P. njalensis* from tree to tree and from plot to plot, even within relatively small areas of uniform, mature cacao. He studied the distribution of the mealybug population in different parts of the tree and found that the canopy, trunk and chupons support 87·2, 9·6 and 3·2 per cent. respectively. No significant considerable variations in mealybug population density on trees from month to month could be detected. He also recorded that the mean number of mealybugs per tree on a plot at the Cacao Research Institute, Tafo, was 65·7, the highest figure on a single tree being 7,371. These figures applied only to that particular plot. In an experiment involving 500 trees carried out at the Institute in the course of the present work, the numbers of mealybugs ranged from 3 to 5,200 per tree, with a mean of 858. The average number of mealybugs per colony ranged from 1 to 150 with an average of 11. In another experiment carried out jointly with the Cacao Research Institute, 16,656 mealybugs were recorded in one tree.

The female of *P. njalensis* is ovoviviparous, producing eggs which hatch into "crawlers" as soon as they are laid, and these tend to live segregated in colonies that are covered by carton tents built by ants. When these crawlers reach maturity, and start to reproduce, the density of population in the colony becomes very high, and some of the newly emerged crawlers migrate to fresh feeding sites, usually towards the growing points of branches, where they form new colonies, which are soon covered by tents.

The area of cacao which was allotted to this work at its outset was just over one acre, containing about 800 trees, at the Cacao Research Institute, Tafo. The level of population on these trees was fortunately very high. All the preliminary experiments had to be made on this plot and fitted into it.

At the beginning of the work, it was thought that the percentage kill obtained in the various experiments could be assessed by the number of mealybugs, both dead and alive, found in the colonies (or " tents ") before and after treatment. It was discovered, however, that the dead mealybugs were not found in the colonies, and in the first few experiments the population after treatment was recorded as a percentage of the average population on the control trees. These control trees were originally incorporated in the experiment for the sole purpose of ensuring that there was no undetected sudden change in the mealybug population during the course of the experiments, caused by climatic or biotic factors. It is reasonable to assume that although this method of assessment was not refined enough to show minor variations in the mealybug population, it provided an adequate indication of the relative efficiency of different chemicals.

In later experiments, however, it was eventually decided to adopt the following methods for assessing the mealybug population:—

1. In the preliminary, small-scale experiments, the number of mealybug colonies on each tree was estimated and where there were 100 or more colonies per tree, a total of 20 to 40 colonies, depending on the number of mealybug counts that were to be made, were taken at random over all the branches of the tree, before and after treatment, and the number of mealybugs inside them counted. On trees with less than 100 colonies, 5 to 15 colonies, according to the number of counts required, were examined and the number of mealybugs in each recorded. The branches carrying the mealybug tents were removed with a tree pruner, and the sections with the tents cut off by secateurs, placed in cylindrical 50-cigarette tins and taken to the laboratory for examination under a binocular microscope. In both cases, the results were assessed by expressing the size of population after treatment as a percentage of that before treatment.

2. In the large-scale experiments, involving trees to the number of 250 to 500 or so, the area was divided into sub-plots of 50 trees, 10 per cent. of the trees, taken at random in each sub-plot, were cut down before treatment, and a further 10 per cent. of the original number, also taken at random, cut down after treatment. The sections of the parts of the tree carrying colonies were cut off, placed in covered tins and immediately taken to the laboratory for examination.

In both cases, control trees were chosen outside the treated plots, to give an indication that there was no undetected drastic change in populations during the course of the experiments. They served no other purpose.

The aim of the primary trials was not to establish the extent to which the mealybug population could be reduced, but to enable a comparison to be made of the effect of the different chemicals and concentrations tested. It was previously mentioned that populations vary considerably from tree to tree, and from one colony to another, but it is suggested, for the following reasons, that the first method was suitable for screening experiments involving a small number of trees:

(a) The plot available for the preliminary work contained only about 800 trees, and it was obvious that the second method of assessment could not be used.

(b) The variation in populations from colony to colony is far less than that from tree to tree.

(c) Since a large proportion of the colonies was examined, the results provided an adequate estimate of populations.

TABLE I.

Spraying experiments with paraoxon, parathion, schradan and dimefox on small trees.

Material	Concentration %	Active material per tree (gm.)	No. of mealybugs alive in 40 colonies (8 colonies per tree) after			Population (as % of the average control) after		
			1 week	2 weeks	3 weeks	1 week	2 weeks	3 weeks
Paraoxon	0·1	0·80	74	—	—	8·9	—	—
	0·07	0·56	65	—	—	7·8	—	—
	0·04	0·32	200	—	—	24·0	—	—
	0·01	0·08	1160	—	—	>100	—	—
Parathion	0·1	0·80	48	—	—	5·7	—	—
	0·07	0·56	83	—	—	9·9	—	—
	0·04	0·32	256	—	—	30·7	—	—
	0·01	0·08	284	—	—	34·0	—	—
Schradan	1·0	8·0	252	104	265	30·7	12·5	31·8
	0·7	5·6	428	572	548	51·1	68·6	65·5
	0·4	3·2	868	740	668	>100	88·8	80·3
	0·1	0·8	1280	816	672	>100	98·0	80·6
Dimefox	1·0	8·0	9	8	37	1·1	1·1	4·4
	0·7	5·6	65	20	172	7·8	2·4	20·6
	0·4	3·2	80	36	240	9·6	4·3	28·8
	0·1	0·8	328	332	444	39·3	39·8	53·4
Control	—	—	684	652	1164 (Average 833)			

Systemic Insecticides used.

The insecticides used in the work described here were

(a) Diethyl p-nitrophenyl phosphate (paraoxon).
(b) O,O-diethyl O-p-nitrophenyl thiophosphate (parathion).
(c) Bisdimethylaminophosphonous anhydride (schradan).
(d) A systemic insecticide, bis(dimethylamino)fluorophosphine oxide (dimefox). In the early experiments, it was known as CR.409. Later it was used in a commercial formulation called Hanane containing 50 per cent. of the active ingredient. In the present work, the dosages refer to the amounts of the active ingredient, dimefox.

Although paraoxon and parathion are not strictly systemic, they are strong contact insecticides, and it was thought desirable to include them in the experiments. The last two chemicals were used by Nicol (1952) in some experiments between the end of 1949 and 1952.

Experiments were carried out concurrently with various possible methods of application, but they will be discussed under the headings of spraying (below), soil treatment (p. 675) and trunk implantation (p. 701).

Spraying Experiments.

From observations on the position of mealybug tents in cacao trees, it was found that out of 377 tents on branches which were growing more or less horizontally, 375 (99·5%) were built on the lower side and two only on the upper side, one of which was covered by another small branch. This appeared to be a contrivance on the part of the ants to protect the colonies from the damaging effect of rain drops on the tents. The position of the tents appeared to be suitable for spraying from the ground.

In the first trial, commenced on 9th May 1950, very small cacao trees were sprayed with 800 cc. of (a) schradan and dimefox, at concentrations of 1·0, 0·7, 0·4 and 0·1 per cent. active material, and (b) paraoxon and parathion at one-tenth these rates. There were five trees per treatment. A bucket-type sprayer was used.

The results are given in Table I, where it will be noticed that trees sprayed with paraoxon and parathion were examined once only, after one week, as they have a rapid contact action. The trees treated with dimefox and schradan were examined after one, two and three weeks because a rather slower action was expected.

Paraoxon, parathion and dimefox gave encouraging results, and thus a second trial was commenced on 22nd June 1950, in which larger trees (about 12 in. in girth) were sprayed by means of a small portable motor sprayer. There were five trees per treatment, and each tree received 1·5 litres of solution.

The figures in Table II show inconsistent results when larger trees are involved. It is not understood why the efficiency increases as the concentration decreases in the spraying trials with dimefox, but this insecticide is highly volatile, and it seems that the trees that gave the higher rate of reduction were under shade, while the others were exposed to the intense heat of the sun, causing the rapid evaporation of dimefox before it could act properly.

Finally, a trial was designed and conducted in the same way as the above experiment, in which paraoxon and parathion were applied at the same rate as schradan and dimefox, namely 1·0 per cent. active ingredient. The results showed that the increase of active material did not give a corresponding increase in the efficiency; the size of population one and two weeks after treatment with paraoxon was 40·7 and 50·2 per cent., respectively, of that before treatment. The corresponding figures following treatment with parathion were 32·6 and 14·9 per cent.

During the course of the above experiments, the following points were noticed:—

(a) A large population of the live mealybugs was found in the crevices of wood that were not accessible to the spray material, thus showing this method of control to be inconsistent and unreliable.

(b) Dead mealybugs were rarely found in the tents on treated trees. Further experiments which will be described later were carried out to determine the fate of these mealybugs.

(c) The trees sprayed with 1 per cent. paraoxon, parathion and dimefox were badly scorched.

It could, therefore, be concluded from the above experiments that spraying did not give satisfactory results.

TABLE II.

Spraying experiments with paraoxon, parathion and dimefox on larger trees.

No. of mealybugs alive in 40 colonies (8 per tree).

Material	Concentration %	Before treatment	After 1 week		After 2 weeks	
			No.	Population as % of that before treatment	No.	Population as % of that before treatment
Paraoxon	0·1	2160	492	22·7	530	24·5
	0·07	1604	609	38·0	804	50·1
	0·05	1460	1273	87·2	1172	80·3
	0·03	1516	818	54·0	1290	85·1
Control	—	1644	1468	—	1472	—
Parathion	0·1	1816	456	25·1	231	12·7
	0·07	1152	568	49·3	381	33·1
	0·05	1648	920	55·8	510	30·9
	0·03	696	592	85·1	576	82·8
Control	—	1608	1480	—	1096	—
Dimefox	1	1772	767	53·3	848	47·8
	0·7	1736	945	54·4	798	36·0
	0·5	1290	381	30·7	405	31·4
	0·3	1686	288	17·1	326	19·3
Control	—	2340	1880	—	1864	—

Soil Treatment with Systemic Insecticides: Laboratory and Insectary Experiments.

Technique.

In carrying out insectary experiments, the artificial infestation of cacao seedlings with mealybugs was not in itself sufficient; to obtain the protective tents, it was necessary to establish the field association between these insects and the *Crematogaster* ants.

The following technique was evolved. Small inverted paper cones were attached round the stem of the seedlings. The cones were then filled with sections of cacao twigs carrying colonies of mealybugs, and at the same time a number of ants were shaken from a nest, constructed in the cavities of dead cacao branches, on to the seedling plant above the cones. The nest was then placed on the soil at the base of the stem of the seedling. The ants quickly realised the whereabouts of the mealybugs, and thus the association was soon established. The migration of the mealybugs to the seedling took place as the sections of twig dried out and after a period of four to seven days there was usually a satisfactory infestation. The twig sections and cones were then removed. The ant nests were collected from mealybug-infested cacao trees, and a continual supply had to be maintained because the ants tended to disappear or become inactive in the insectary where the seedlings were kept during infestation.

The introduction of ants into the insectary had the further effect of producing a higher percentage establishment of mealybugs. This fact was illustrated by the following experiment. Each of eight one-year-old seedlings in individual bamboo pots was fitted with a paper cone containing twig sections bearing approximately 200 mealybugs. Ant nests were placed round four of these seedlings and the stems of the other four were encircled at the base with a tanglefoot band which excluded ants from the mealybug-infested region. The results are shown in Table III.

TABLE III.

The effect of the presence of *Crematogaster* ants on the establishment of mealybugs.

Ants	Approximate no. of mealybugs which left twig sections					Exact no. of mealybugs established on seedlings				
	1	2	3	4	Total	1	2	3	4	Total
Absent ..	174	198	175	162	709	68	16	61	26	171
Present ..	159	198	172	200	729	65	91	212	102	470

It was found finally that the construction of tents by ants on infested insectary plants could be encouraged by the simple procedure of placing the plants and ant nests outside the insectary on the ground in the shade under trees. In a comparatively short time, tents had been constructed and were maintained even when the plants were returned to the insectary.

The conditions required for the construction of tents are not fully understood. Undoubtedly, the abundance of suitable vegetable débris outside as opposed to inside the insectary is an encouragement to the ants, but the need for protection of the mealybugs outside is probably the critical factor. This may be borne out by the fact that tents were frequently built in one to four days over established colonies when heavy rain penetrated to the mother plants through the wire screening in the roof of the insectary. Similar colonies on plants beneath the glass sections of the roof were only rarely covered.

This phenomenon was also noticed in the field during the artificial infestation of cacao trees. If the relative portion of the branch was not covered with an umbrella-like paper cone (see Pl. XXI, fig. 2), the mealybugs, on becoming established, were soon covered by tents. Where cones covered the infested portion, tents were not usually found, although establishment still took place.

Preliminary experiments.

On 2nd May 1950, two artificially infested cacao seedlings, about 10 months old and grown in individual bamboo basket pots, were used for each of the four insecticides and two remained untreated. Paraoxon and parathion were applied at the rate of 0·1 gm. in 100 cc. solution, and schradan and dimefox at the rate of 0·5 gm. in 100 cc. solution. The solutions were applied to the soil in a slight depression round the stem of the seedlings. It was not possible to count the mealybugs inside the tents, but a count of the number of established colonies before treatment indicated that the seedlings were highly infested. The results, assessed four days after treatment, are shown in Table IV.

The complete disappearance of mealybugs from the two plants treated with dimefox was surprising, and had to be confirmed. On 8th May 1950, five seedlings about 11 months old were artificially infested with mealybugs and ants and then treated with 0·5 gm. dimefox in 100 cc. solution. Another five similar seedlings remained untreated. Nineteen colonies became established on the treated seedlings and 18 on the untreated ones. All ten plants were examined four days later, and it was again found that all the tents on the treated plants were empty. On the untreated plants there was a total of 207 mealybugs, one of which was dead. Further work, to be described later, showed that the mealybugs died in the tents and were then removed by the ants.

TABLE IV.

Preliminary experiment with soil treatment using paraoxon, parathion, schradan and dimefox.

Material	Concentration %	Active material per plant (gm.)	No. of colonies established on the 2 seedlings	No. of mealybugs found after treatment	
				Live	Dead
Paraoxon	0·1	0·1	16	211	3
Parathion	0·1	0·1	18	259	6
Schradan	0·5	0·5	6	107	0
Dimefox	0·5	0·5	17	0	0
Control	—	—	10	87	0

These two experiments were the first to illustrate the successful use of dimefox for the control of cacao mealybugs by root uptake. Further investigations which led to the large scale field trial already reported (Hanna, Heatherington & Judenko, 1952) will now be discussed.

On 4th July 1950, an experiment was conducted to find out whether soil treatment with paraoxon and parathion at higher rates than hitherto employed would be effective in controlling mealybugs. Solutions of these chemicals, containing 1·0, 0·7 and 0·4 gm. active ingredient in 100 cc., were applied at the rate of 100 cc. per ten-month-old seedling, grown in locally made basket pots; two plants were used for each insecticide and another two for control. All the seedlings were artificially infested with mealybugs and ants. The seedlings were examined two weeks after treatment and the results are shown in Table V.

TABLE V.

Soil treatment with paraoxon and parathion using higher rates.

Active material per plant (gm.)	Paraoxon				Parathion			
	No. of colonies		No. of mealybugs found after treatment		No. of colonies		No. of mealybugs found after treatment	
	Before treatment	After treatment	Alive	Dead	Before treatment	After treatment	Alive	Dead
1	14	4	3	1	21	9	94	6
0·7	13	8	138	0	19	13	115	2
0·4	12	5	71	2	19	10	193	0
Control	15	23	658	1	18	21	372	36

An appreciable reduction in the number of colonies occurred in all treatments, but the number of live mealybugs that still remained on the plants indicated that these chemicals were unsatisfactory for controlling a virus vector, when the mortality rate must be of a very high order.

It was noticed that when the mealybug tents became empty, the ants did not maintain them and they consequently crumbled after a few days and were eventually washed down by rain.

Between 2nd May and 24th July 1950, a number of insectary experiments were carried out using dimefox, covering a range of quantities of active ingredient per plant in different volumes of solution.

The seedlings used were 10–12 months old and heavily infested with mealybugs by the technique previously described. Ants were always present. The results are summarised in Table VI.

TABLE VI.

Soil treatment with dimefox using different concentrations.

Active material per plant (gm.)	Amount of solution per plant (cc.)	Concentration %	Interval between treatment and examination, in days	No. of plants used	No. of colonies		No. of mealybugs found after treatment	
					Before treatment	After treatment	Alive	Dead
0·5	100	0·5	2	2	14	0	0	0
0·25	100	0·25	2	3	12	0	0	0
0·2	2·0	10·0	2	1	8	0	0	0
0·15	3·0	5·0	5	1	11	0	0	0
0·1	1·0	10·0	5	1	6	0	0	0
0·1	100	0·1	4	4	19	0	0	0
0·075	1·5	5·0	5	1	4	0	0	0
0·05	100	0·05	4	4	32	3	6	3
0·02	0·1	20·0	6	2	7	0	0	0
0·01	0·05	20·0	6	2	5	0	0	0
0·005*	0·05	10·0	7	2	18	0	0	0
Control	—	—	3	3	32	33	552	3
Control	—	—	9	3	10	11	157	0

* Applied directly to an exposed root, not to the soil.

It was concluded from the above data that (a) very effective initial kills can be obtained using dimefox at dosages as low as 0·005 gm. active ingredient per seedling plant, and (b) there appears an indication, within the range employed, that the concentrations of the solution are unimportant in the treatment of seedlings.

It is of interest to note the approximate ratio between the weights of chemical and of seedlings in an experiment carried out on the 10th July 1950, in which the dosage of 0·005 gm. per plant was again employed with a satisfactory result:—

Plant	Girth (cm.)	Ratio active ingredient in gm. to girth in cm.	Wt. of plant (gm.)	Approx. ratio wt. inactive ingredient : wt. plant
1	3·6	1 : 720	60·3	1 : 12,000
2	3·2	1 : 640	69·4	1 : 14,000

Persistence of insecticidal action of dimefox within seedling plants.

Uninfested one-year-old seedlings in bamboo baskets were treated with 100 cc. of a solution of dimefox at concentrations of 1·0, 0·7 and 0·4 per cent. active ingredient. Two plants were used for each treatment and two for control. After seven days, each plant was infested with 60 colonies of mealybugs by the paper-cone technique; five days later, the plants were examined and the numbers of mealybugs recorded.

The plants were again infested and examined after a further seven days. This process was repeated at intervals, and the final examination took place 67 days after treatment. The percentage establishment on treated plants was calculated from the figure for establishments on the control plants, which was taken as 100 per cent. The results are shown in Table VII and, as it was considered that plants that showed an establishment of less than 10 per cent. were still toxic, the persistency period for all three concentrations was approximately 50 days.

TABLE VII.

Persistence of insecticidal action of dimefox within seedling plants.

	Concentration %	Interval in days between treatment and examination								
		12	19	26	33	40	46	53	60	67
No. of mealybugs on examination	1·0	0	1	0	1	9	16	41	100	112
	0·7	0	0	2	7	4	19	74	194	88
	0·4	1	0	2	8	12	97	328	227	142
	Control	233	195	143	247	126	276	601	231	136
Percentage establishment	1·0	0	0·5	0	0·4	7·1	5·8	6·8	43·3	82·3
	0·7	0	0	1·4	2·8	3·2	6·9	12·3	84·0	64·7
	0·4	0.4	0	1·4	3·2	9·5	35·2	54·6	98·3	>100
	Control	100	100	100	100	100	100	100	100	100

On 14th July 1950, a similar experiment, using two plants per treatment, was carried out in which lower concentrations of dimefox were used. Results are shown in Table VIII; plants treated with 100 cc. of 0·3 and 0·2 per cent. active ingredient remained toxic to mealybugs for approximately four weeks, while plants treated with 0·1 per cent. active ingredient remained toxic for about 2–3 weeks.

TABLE VIII.

Persistence of dimefox in seedlings when used at lower concentrations.

	Concentration %	Interval between treatment and examination				
		13 days	20 days	27 days	34 days	41 days
No. of mealybugs on examination	0·3	2	3	6	39	268
	0·2	0	2	8	41	223
	0·1	0	27	42	153	245
	Control	379	219	182	138	264
Percentage establishment	0·3	0·5	1·4	3·3	28·3	>100
	0·2	0	0·9	4·4	29·7	84
	0·1	0	12·3	23·1	>100	93
	Control	100	100	100	100	100

As a result of these experiments, it appears that to obtain satisfactory control of mealybugs on seedling plants with dimefox, for the appreciable period of six weeks, it is necessary to apply 0·4 to 0·7 gm. active material per plant, a figure which is considerably higher than that required to give initial kill, *viz.*, 0·005 gm. per plant.

Phytotoxicity.

The phytotoxic effect of dimefox on cacao seedlings was determined for a range of dosage rates. One-year-old plants were treated with varying quantities of a 20 per cent. solution of dimefox and closely observed for a period of seven weeks, during which time records were made of leaf fall. The results are shown in Table IX; it was found that no damage occurred when dimefox was applied up to the rate of 0·02 gm. per plant, but that at the higher dosages of 0·1 to 1·0 gm. per plant, leaf fall occurred to the extent of 50 to 100 per cent. However, none of the plants died and those leaves which developed after treatment were unaffected.

TABLE IX.

Test of phytotoxicity.

Active material per plant (gm.)	Girth of plant tested (in.)	No. of leaves: Before treatment	No. of leaves: 7 weeks after treatment	% of leaves shed
1	1·5	14	0	100
0·8	1·5	22	0	100
0·6	1·5	14	0	100
0·4	1·4	22	1	96
0·2	1·5	14	10	71
0·1	1·5	24	12	50
0·02	1·7	33	30	9
0·01	1·2	20	19	5
Control	1·5	19	17	11

The fate of dead mealybugs.

In the soil treatment experiments, Tables IV–VI, the tents on those plants that had been treated with dimefox were found to be empty. If this treatment was to be regarded as a possible control measure, it was necessary to account for the disappearance of the mealybugs.

Knowledge of the activities of the attendant ants suggested that they might be responsible for the disappearance of the mealybugs, and that if the ants were absent, dead mealybugs would be found in the colonies. The two following experiments showed that this supposition was justifiable.

A large paper disc was fitted around the base of the stems of three artificially infested cacao seedlings. Tape covered the join of the disc, which was sealed to the stem with wax; a band of tangle-foot was drawn round the circumference of the disc. These measures were taken to exclude ants, and to catch mealybugs leaving or dropping from the plant. Two of the plants were then sprayed three times with a 2 per cent. solution of DDT emulsion, which killed those ants present on the plant above the disc. The third plant was sprayed with water but remained otherwise untreated throughout the experiment. Finally, one of the two sprayed plants was treated with 0·2 gm. dimefox applied to the soil in 100 cc. of solution. After 24 hours, all the plants were examined. The results, shown in Table X, showed that in the absence of ants, dead mealybugs are found.

In a second experiment, which was carried out in the field, two naturally infested small cacao trees were sprayed several times with a solution of 0·2 per cent. γ BHC (applied as crude BHC containing 13% γ isomer), and at the same time a tangle-foot band was made round the base of one of them. This tree, after an interval of one week, was then sprayed with a 0·5 per cent. solution of dimefox. After a further interval of one week, both trees were examined for mealybugs by taking from each a random sample of 20 colonies. The tree which was sprayed with BHC only acted as a control, and in the 20 colonies, a total of 342 mealybugs were found, of which 341 were alive. In the second tree, the total number of mealybugs in the sample was 172, of which only eight were alive. Again, therefore, in the absence of ants, dead mealybugs were found in the colonies.

TABLE X.

Removal of dead mealybugs by *Crematogaster* ants.

Details	Control	DDT only	DDT+dimefox
Live mealybugs on plant and disc	68	56	0
Dead mealybugs on plant	0	0	64
Dead mealybugs on disc	0	7	4
Mealybugs on sticky band	0	0	0
Ants	Present	Absent	Absent

The occurrence of empty tents on plants treated with dimefox was now understood to be due to the removal of the dead mealybugs by ants. Further work had still to be carried out, however, since the possibility could not be excluded that ants were removing not only dead, but also live mealybugs, to nearby untreated host plants. Two experiments were designed to investigate this possibility.

In the first experiment, seven one-year-old seedlings were artificially infested with both mealybugs and ants, sprayed with dimefox, and immediately placed with nine untreated mealybug-free seedlings, alternating with one another. The foliage of all plants was in close contact. On examination, it was found that the mealybugs had disappeared completely from the treated plants, but none of the untreated plants was infested. The dimefox spray did not affect all the ants, as there was still a certain amount of activity at the end of the experiment. In the second experiment, carried out jointly with the Cacao Research Institute, four cacao seedlings were examined and 1,602 mealybugs recorded on them. Dimefox at the rate of 25 cc. 0·1 per cent. solution was applied to the soil round the stem, and the plants were immediately surrounded with 30 mealybug-free seedlings. Ants were active over all plants. After two days, a second examination was made; only 11 mealybugs were found on the four treated plants, and none on the 30 encircling ones.

It was thus concluded that ants do not carry live mealybugs from dimefox-treated plants to more favourable hosts, but only remove the dead insects from the colonies. In assessing the effect of dimefox treatment, it was therefore not incorrect to assume that the total disappearance of mealybugs indicated a 100 per cent. reduction.

Field Experiments.

Technique of application of systemic insecticides to the soil.

The following method of applying the chemical to the soil was used in the preliminary investigations with the four insecticides, and in the detailed research programme with dimefox. Food plants growing within four feet of the trunk were removed to avoid any toxic hazard to anyone that might have eaten them. and the solution poured into a slight depression made in the soil immediately round the base of the trunk (Pl. XXI, fig. 3). In order to check evaporation of the chemical, the depression was afterwards filled with soil or covered with fallen cacao leaves.

When results showed that a control measure for cacao mealybugs was possible, a more practical and simplified technique was evolved. Removal of food plants (cocoa yam, *Xanthosoma sagittifolium*, grown by African farmers for food), and the making of a slight depression, were carried out as before, but instead of watering the soil with the solution, capsules with water-soluble walls (Pl. XXI, fig. 4), which collectively contained the required quantity of active ingredient, were inserted horizontally and immediately covered with soil. The insecticide was liberated as these capsules were dissolved by the soil moisture. This second method had the added advantage that it permitted the insecticides to be more safely handled.

Investigations with various insecticides.

Field work was commenced on the 11th May 1950, when four average-sized trees were used for each of the following treatments: paraoxon and parathion at 0·1 per cent. active material, schradan and dimefox at 1·0, 0·7, 0·4 and 0·1 per cent. active material. Four litres of each solution were applied per tree. Four trees remained untreated. Mealybugs were recorded for every tree, at each examination, from a total of ten colonies taken at random from all branches and the result was calculated as a percentage of the average figure obtained on the control trees, as shown in Table XI.

TABLE XI.

Field experiment with paraoxon, parathion, schradan and dimefox applied to the soil.

Material	Conc. %	No. of mealybugs alive in 40 colonies after			Population (as % of the average control) after		
		1 week	2 weeks	3 weeks	1 week	2 weeks	3 weeks
Paraoxon	0·1	606	688	608	83·2	94·5	83·5
Parathion	0·1	587	637	1530	80·6	87·5	>100
Schradan	1·0 0·7 0·4 0·1	351 382 816 698	308 574 565 774	699 524 526 604	48 52·4 >100 95·8	42·3 78·8 77·6 >100	96 72 72 83
Dimefox	1·0 0·7 0·4 0·1	23 284 306 531	1 8 25 489	1 1 2 445	3·1 39 42 72·9	0·1 1·0 3·4 67·1	0·1 0·1 0·3 61·1
Control	—	720	764	700 (Average 728)			

The treatment with dimefox showed a marked superiority, but, as in the insectary experiments, a further trial was conducted with paraoxon and parathion applied at the increased rate of 4 litres per tree of a solution containing 1 per cent. active material. This experiment was similar in design to the one above, in the number of both trees and colonies taken per examination. Post-treatment counts were made after four and six weeks, as intermediate experiments with dimefox had shown that the chemical gave good kill up to this period. The results were assessed by the size of population after treatment expressed as percentage of that before treatment, as shown in Table XII. They indicate that neither paraoxon nor parathion is comparable with dimefox in controlling mealybugs.

TABLE XII.

Field experiments with paraoxon and parathion applied to the soil at higher rates.

Material	No. of mealybugs recorded in a total of 40 colonies			Population (as % of that before treatment) after	
	Before treatment	After treatment			
		4 weeks	6 weeks	4 weeks	6 weeks
Paraoxon	1273	1258	1853	98·9	>100
Parathion	1356	1303	1413	96·1	>100
Control	1256	1860	1860	>100	>100

The experience so far obtained showed that it was simple to apply the insecticide by the soil treatment method. The distribution of the insecticide within the tree appeared to be uniform and preliminary results showed that an encouraging degree of control could be obtained using dimefox. There was, however, one undesirable factor, namely, the large amount of water required per tree. Many cacao farms which would require treatment are situated at a considerable distance from any available supply of water. Owing to the scarcity of motorable roads, treatment in such areas would involve the "head loading" of all water requirements. Thus a control measure requiring approximately 1 gallon per tree (*i.e.*, 600 gal. per acre) could not be widely adopted. It was, therefore, desirable to experiment with a more concentrated form of dimefox.

Development of the soil treatment with dimefox.

(a) *Preliminary experiments on dosage rates.*

Between 13th June and 19th July 1950 some field experiments were conducted with dimefox to find out the relative importance of the weight of active material per tree, and of the concentration and volume of the solution applied.

Each treatment was repeated on four trees with an average girth of about 14 in.; the insecticidal effect was estimated from records of the number of mealybugs in pre-treatment and post-treatment samples of 160 colonies (40 per tree). The results of the experiments are collectively tabulated in Table XIII. The results showed that the mortality increased with the weight of active material and the indication was that, provided the weight of active material was unchanged, similar results could be obtained with either high or low concentrations, high degrees of control being attained even when only small quantities of water were used.

It was desirable, at this stage, to find the exact amount of active material necessary for effective control. It was obvious that the larger the tree, the more active material it would require. Trees vary considerably in size on a single cacao farm and a fixed dose per tree would thus be wasteful, in that the quantity of

TABLE XIII.

Soil treatment with dimefox using different volumes and concentrations.

Wt. of active material per tree (gm.)	Volume of solution applied per tree (cc.)	Concentration of solution %	No. of mealybugs in 160 colonies (40 per tree)		Population as % of that before treatment
			Before treatment	After treatment	
16	80	20	1437	5	0·3
16	4000	0·4	2494	20	0·1
8	40	20	2203	201	9·1
8	4000	0·2	1817	99	5·4
4	20	20	1884	495	26·3
4	4000	0·1	1848	519	28·1
Control	—	—	1740	1400	—

Total rainfall during the experiment, 4·29 in.

active material would be governed by the size of the largest tree. It was necessary to have a dosage rate based on some measurement of tree size. As has been mentioned earlier, the girth was the measurement used, and in order to standardise the procedure it was taken 1 ft. above ground level and recorded in inches. When branching occurred at less than 1 ft. above the soil level, each branch was considered as a separate tree.

An experiment was commenced on 14th August 1950, in which amounts of 0·4, 0·6, 0·8 and 1·0 gm. dimefox per in. of girth were applied in solutions of 1, 2 and 4 per cent. Each treatment was repeated on eight trees and the results recorded four weeks after application (Table XIV).

TABLE XIV.

Effectiveness of dimefox applied to the soil at rates proportional to the girth of the trees.

Concentration %	Active material per in. girth (gm.)	No. of mealybugs alive in 80 colonies (10 per tree)		Population as % of that before treatment
		Before treatment	After treatment	
1	1	749	18	2·4
	0·8	758	112	14·8
	0·6	876	357	40·7
	0·4	882	106	12·0
	Control	1060	1214	>100
2	1	380	12	2·2
	0·8	1286	174	13·5
	0·6	618	68	11·0
	0·4	477	216	45·3
	Control	739	883	>100
4	1	739	8	1·1
	0·8	969	42	4·3
	0·6	1326	80	6·0
	0·4	559	131	22·4
	Control	654	1487	>100

Total rainfall during the experiment, 1·2 in.

TABLE XV.

Effectiveness of dimefox used at higher rates.

Treatment gm. per in. girth	No. of mealybugs in a total of 240 colonies (10 per tree)		Population as % of that before treatment
	Before treatment	After treatment	
1·2	3279	253	7·7
1·4	4374	209	4·2
Control (100 colonies)	1344	1712	>100

Total rainfall during the experiment, 7·9 in.

Although 1 gm. dimefox per in. of girth gave good results, it was necessary to aim at a higher percentage kill because of the insect-virus association. Higher amounts of active material were, therefore, tested in an experiment commenced on 11th October 1950. Two lots of 24 trees received, respectively, 1·2 and 1·4 gm. dimefox per in. of girth, applied in 10 per cent. solution, ten trees remained untreated and mealybugs were counted in ten colonies taken at random from each tree before and after treatment. Results, recorded six weeks after application of the treatments, were disappointing (Table XV), and the experiment was repeated in a similar manner on 9th November 1950, using 20 trees for each treatment and eight trees for control (Table XVI).

TABLE XVI.

Repetition of the previous experiment.

Treatment gm. per in. girth	No. of mealybugs in a total of 200 colonies (10 per tree)		Population as % of that before treatment
	Before treatment	After treatment	
1·2	2648	127	4·8
1·4	3267	128	3·9
Control (80 colonies)	1171	1068	91·1

Total rainfall during the experiment, 3·4 in.

The size of population as a percentage of that before treatment in these two experiments (Tables XV and XVI) was higher than previously observed with only 1 gm. per in. of girth (Table XIV), which was an unexpected contradiction. It was of the utmost importance to account for this drop of efficiency, and the following points were considered:—

(i) The average girths of the trees used in the three experiments were 15, 11·8 and 11 in., respectively, and the size of tree could therefore be eliminated as a factor.

(ii) If the soil conditions were variable, the more porous patches might have allowed a greater percolation of the chemical away from the region of the absorbent roots, leading to a smaller percentage reduction of population on individual trees and thus to a lessening of the total effect of the

TABLE XVII.

Large-scale experiments using 1·2 and 1·6 gm. dimefox active material per in. of girth.

	A		B			A		B			A		B	
Sub-plot	Girth (in.)	No. of mealybugs	Girth (in.)	No. of mealybugs	Sub-plot	Girth (in.)	No. of mealybugs	Girth (in.)	No. of mealybugs	Sub-plot	Girth (in.)	No. of mealybugs	Girth (in.)	No. of mealybugs
1	7	1385	7·5	1	2	9	756	20	447	3	7	458	8·5	3
	10	996	12·5	28		15	3331	8·5	0		5·5	450	10	5
	12	802	16	93		9	417	15	38		6	210	6	0
	9·5	838	6·5	2		20	1194	7	0		5·5	147	5	0
	15·5	3123	6·5	0		8	4887	9	0		6	358	7	0
Totals		7144		124			10585		485			1623		8
4	6	299	6	0	5	4	0	9·5	0	6	13·5	3458	6	0
	6·5	24	5	0		5	1317	6	0		11·5	2838	13·5	3
	6	381	6	0		13·5	4517	6	1		6	217	7	0
	7	308	9·5	0		8	1248	8	0		5	109	5·5	0
	6	22	7	0		7·5	71	11·5	3		6	1069	6	0
Totals		1034		0			7153		4			7691		3
7	7·5	770	3·5	0	8	12·5	3027	7	1	9	4	11	3·5	0
	6·5	201	8	0		7	98	10·5	12		7	654	8	24
	6·5	257	7	35		5·5	271	6	41		13	864	13	8
	6	249	9	14		7	388	7·5	1		7·5	0	13	0
	8	1220	7	2		6	372	5	0		13	1431	10	5
Totals		2697		51			4341		55			2960		37
10	8	996	19	227	Control	6	0	6·5	0					
	3	105	6·5	0		13	960	13·5	6124					
	21	3643	12	1		5·5	625	5·5	961					
	14·5	2647	15·5	4		6	342	6	709					
	12	4	9	0		6	200	7	0					
Totals	7395			232			2127		7794					

The results are summarised in Table XVIII.

A: Trees cut out and examined before treatment.
B: Trees cut out and examined 6 weeks after treatment.

treatment. All the trees that had been used in the October experiment (Table XV) were, therefore, given 4 litres of water applied to a depression round the base of the trunk, and the time taken for it to disappear was recorded. It was clear that there was no apparent correlation between the permeability of that particular soil and the degree of reduction of mealybug population.

(iii) Chemical analysis showed that the dimefox had not deteriorated.

(iv) Rain may have caused leaching of the dimefox to a point beyond the reach of the roots, or it may have caused decreased transpiration, and thus indirectly have reduced uptake of dimefox. It can be seen that there was more rainfall during the October than during the November experiment, and considerably more than during the one in August.

In the above three experiments, therefore, the size of population after treatment seems to indicate that heavy rains may cause the leaching of the insecticide, but not to an appreciable extent.

(b) *Experiments to obtain higher percentage kills.*

Previous experiments had involved only a few trees per treatment, and it was thought advisable to conduct a larger field trial. An area was selected which contained 500 trees, and this was divided into ten sub-plots of 50 trees each. The trees in five sub-plots were treated at the rate of 1·2 gm. dimefox per in. of girth and those in the remaining five at 1·6 gm. The treatment examinations were conducted on whole trees, five trees (10%) from each sub-plot being selected by a randomised method for each examination. To show that there was no sudden undetected decrease in the natural population of mealybugs, ten trees outside the plot were selected, five of which were cut down before treatment started and the other five after treatment. After the trees were cut down, all the sections containing colonies were removed to the laboratory, where the mealybugs were counted. Post-treatment examinations were made after six weeks. Results are detailed in Table XVII, in order to illustrate the range of variation in mealybug populations, and summarised in Table XVIII.

TABLE XVIII.

Summary of data in Table XVII.

Treatment gm. dimefox per in. girth	Sub-plot	No. of mealybugs on 5 trees		Population as % of that before treatment
		Before treatment	6 weeks after treatment	
1·2	1	7144	124	1·7
	2	10585	485	4·5
	3	1623	8	0·5
	4	1034	0	0
	5	7153	4	0·1
	Total	27539	621	2·2
1·6	6	7691	3	0·04
	7	2697	51	1·9
	8	4341	55	1·3
	9	2960	37	1·2
	10	7395	232	3·1
	Total	25084	378	1·5
Control	Total	2127	7794	—

Total rainfall during the experiment, 2·74 in.

The results were still not considered sufficiently satisfactory. From examinations on individual trees, it was found that the majority of the live mealybugs found after treatment were on big trees (see Table XVII). Of the 621 mealybugs recorded after six weeks on the first five sub-plots, 447 were found on a 20-in. tree, 93 on a 16-in. tree, 38 on a 15-in. tree, and 28 on a 12½-in. tree. The remaining 15 were on six trees, each of which was less than 10 in. in girth. All the trees less than 6 in. in girth were free from mealybugs after treatment, and it seems safe to assume that 8 gm. dimefox (1·6 gm. per in. of girth) is sufficient to clear the mealybugs from 5-in. girth trees.

Further detailed experiments were made to find whether further reduction in numbers, especially on large trees, could be obtained by gradually increasing the amount of active material, until satisfactory control was attained.

Three groups of heavily infested cacao trees were selected with girths of 10, 15 and 20 in., respectively, each group consisting of 12 trees, which were subdivided into three lots of four trees that received a different dosage. Trees having a girth of 10 in. were treated with 1·5, 2 and 2·5 gm. dimefox per in. of girth, the 15-in. trees were given 2, 2·5 and 3 gm. per in. of girth, and the 20-in. trees were given 2·5, 3 and 3·5 gm. Four trees were left as controls. Six weeks after treatment, the results were as shown in Table XIX.

TABLE XIX.

Soil applications of dimefox at varying dosage—girth rates.

Girth (in.)	Dosage gm. per in. of girth	Approximate dosage per tree (gm.)	No. of mealybugs in 160 colonies (40 per tree)		Population as % of that before treatment
			Before treatment	After treatment	
9·5–10	1·5 2 2·5	15 20 25	2313 2070 3036	79 0 0	3·4 0 0
14·5–15	2 2·5 3	30 37·5 45	2523 1749 2121	147 6 0	5·8 0·3 0
19·5–20	2·5 3 3·5	30 60 70	4260 2124 3225	112 22 0	2·6 1·0 0
Control	—	—	1391	1637	—

From the above two experiments, it seemed that the approximate amounts of active material required to give efficient mealybug control were as follows (girth being measured 1 ft. above soil level):—

Girth (in.)	Dosage (gm.)
5	8
10	20
15	39
20	70

(c) *Dosage based on girth—weight correlation.*

It is generally accepted that the quantity of a poisonous material required to kill an animal is proportional to the weight of the latter. Attempts were made to establish a similar relation for treating cacao with dimefox so as to render the cell sap toxic to mealybugs. For field application, it was first necessary to establish a correlation between the girth of the tree, measured one foot above the soil, and its weight. Only the aerial part of the tree was considered and the actual weights were obtained of 428 trees of different girths (from 5 to 30 in.). An estimated weight of the aerial part of the tree, the upper and lower limits, was worked out by the following formula:—

$$\log_{10} Y = -0{\cdot}9412 + 2{\cdot}5296 \log_{10} X$$

where X = girth in in. and Y = weight in lb. (see fig. 1).
It was found that the value of the correlation between the tree weights calculated by the above formula and the actual weights was $r = +0{\cdot}9829$.

If the dosages were to be adjusted in relation to the weight of the trees, it was necessary to know whether the chemical would be expected to be evenly distributed throughout the whole tree, irrespective of its size. In many other trees, heartwood is formed and becomes a central supporting column which is not directly involved in translocation. If the central core, in big trees, has no active part in translocation, then an amount of dimefox based on the total weight of the tree would be unnecessarily large. Determinations were therefore made of the moisture contents of both heart- and sap-wood of cacao trees of different girths, and also the moisture content of their entire cross section. Percentage moisture figures were estimated from four samples of trees of 5, 10, 15 and 20 in. girth.

The analyses showed that in cacao trees, the moisture contents of both the heart- and sap-wood, and also of the cross-sections of trees of different sizes, are approximately the same, being about 55 per cent. Therefore, to obtain the required concentration of dimefox, one must consider the total weight of the tree.

This indicates that in the preliminary experiments, when dimefox was applied at a fixed rate per in. of girth, large trees were receiving smaller amounts of active material per unit of weight, than small trees; this accounts for the low percentage reduction of mealybug population recorded on the big trees. It can be seen by plotting the weight of the trees and the amount of effective active material required per in. of girth, which was recorded in Table XIX for 5, 10, 15 and 20 in. girth, that an increase of 0·1 gm. active material per in. of girth is necessary for every 10 lb. increase in the weight of the aerial parts of the trees.

To test the efficiency of the dosages prescribed by this girth—weight correlation (fig. 1), a large-scale trial under field conditions was designed. Five hundred trees with girths ranging from 3·5 to 18·5 in. were divided into ten sub-plots of 50 trees each. A 5 per cent. solution of dimefox was applied according to the rates in fig. 1. Estimation of the insecticidal effect was determined by cutting down, at random, five trees (10%) from each sub-plot before treatment and another five, six weeks after treatment. The sections carrying mealybugs were placed in covered tins, taken to the laboratory and examined under the binocular microscope. A separate plot of 50 trees acted as a control, to give an indication whether any marked decrease of mealybug population took place during the experiment. Five of these trees, taken at random, were cut down before the treatment and another five after it, and the population counted. The results are recorded in Table XX.

The total number of mealybugs in the random sample of 50 trees examined before treatment was 42,971 and the total number of mealybugs in the random sample of 50 trees examined six weeks after treatment was 35. The population after treatment as a percentage of that before treatment was 0·08.

This experiment was then continued in order to establish whether trees could be kept virtually free of vectors for six months, a period which was thought at the time to be the maximum for latent infection by the virus. Further treatments were accordingly carried out on the remaining trees, and population counts

TABLE XX.

Large-scale field experiment using dosages of dimefox based on the girth—weight correlation.

Sub-plot	No. of mealybugs on each tree*		Sub-plot	No. of mealybugs on each tree*	
	Before treatment	6 weeks after treatment		Before treatment	6 weeks after treatment
1	900	0	2	627	0
	347	0		3164	0
	814	0		88	1
	659	1		378	0
	280	0		76	1
Total	3000	1	Total	4333	2
3	2258	2	4	956	0
	367	0		190	0
	1003	1		1379	1
	134	0		294	4
	3	1		843	1
Total	3765	4	Total	3671	6
5	1441	1	6	533	0
	1672	1		907	0
	686	0		405	0
	1326	0		193	0
	1352	0		386	0
Total	6477	2	Total	2424	0
7	842	1	8	284	7
	2163	0		491	0
	5200	2		667	0
	860	0		445	0
	821	0		360	2
Total	9886	3	Total	2247	9
9	560	0	10	275	0
	715	1		858	7
	53	0		168	0
	720	0		1287	0
	2410	0		122	0
Total	4458	1	Total	2710	7
Control	83	681			
	508	107			
	1	637			
	1101	2974			
	1324	1570			
Total	3017	5969			

Total rainfall during the experiment, 5·73 in.

* Five trees were examined before treatment and another five after it: the figures "before" and "after" treatment thus refer to different trees.

made on successive samples of them, at the following intervals after the original application:—

(*a*) 100 trees (*i.e.*, all those left on 2½ sub-plots) were treated twice more, at 8 and 16 weeks, and counts made on successive randomised samples of 10 trees, taken at 8, 16 and 24 weeks.

(*b*) 100 trees (*i.e.*, all those left on a further 2½ sub-plots) were treated once more, at 12 weeks, and counts made on successive randomised samples of ten trees at 12 and 24 weeks.

(*c*) 200 trees (*i.e.*, all those left on the remaining 5 sub-plots) were left without further treatment, in order to find the rate of build-up of the population that survived the original application, and counts made on successive randomised samples of 20 trees at 6, 12, 18 and 24 weeks.

TABLE XXI.

Number of treatments required to keep the trees free for 6 months.

Treatment every	Pre-treatment count (10 trees)	After 8 weeks (1 treatment)	Population as % of that before treatment	After 16 weeks (2 treatments)	Population as % of that before treatment	After 24 weeks (3 treatments)	Population as % of that before treatment
(*a*) 8 weeks	6966	62	0·9	84	1·2	45	0·6
		After 12 weeks (1 treatment)		After 24 weeks (2 treatments)			
(*b*) 12 weeks	13496	306	2·3	765	5·7		

Where counts and treatments fell on the same week, the former were made immediately before the latter. The original populations in the three groups, (*a*), (*b*) and (*c*), were computed from the original pre-treatment counts made on the sub-plots concerned. The results are shown in Tables XXI and XXII.

TABLE XXII.

The build-up from mealybugs surviving after one treatment.

Pre-treatment count (20 trees)	After 6 weeks	Population as % of that before treatment	After 12 weeks	Population as % of that before treatment	After 18 weeks	Population as % of that before treatment	After 24 weeks	Population as % of that before treatment
(*c*) 15408	16	0·1	388	2·5	1439	9·4	1637	15·5

The above experiments (Tables XX–XXII) showed that:—

(i) The application of dimefox to the soil round the trunk in dosages based on the girth—weight correlation prescribed in fig. 1 reduced the population of mealybugs to a very low level.

(ii) Three soil applications at eight-week intervals kept the mealybug population at a very low level for six months.

(iii) After one dimefox application, the population rose from 0·1 to 15·5 per cent. of that before treatment in six months. This indicates that the build-up of mealybug population after one treatment is rather slow.

(d) *Persistence of insecticidal action of dimefox within the tree.*

The persistence of insecticidal action within the tree was demonstrated by recording the percentage establishment of mealybugs on trees artificially infested in three experiments at different dates. The trees were considered to be still toxic when there was less than 10 per cent. establishment. The details of the three experiments were as follows:—

(i) 17 trees of 5–8 in. girth were watered with 10 per cent. dimefox at the rate of 1·2 gm. active material per in. of girth. Three treated trees and another three for control were used for each of the seven infestations, some trees being used more than once. No mealybugs or ants were present on the trees before the start of the experiment. A small inverted paper cone was placed on each of two small branches on each tree, and a number of small pieces of twigs from seedlings that were artificially infested with mealybugs in the insectary were placed in them. Each cone was protected from rain by a second umbrella-like cone. One or two ant nests were put on each tree. The results are shown in Table XXIII; the plants evidently remained toxic for about five weeks after treatment.

TABLE XXIII.

Persistence of dimefox at 1·2 gm. per in. of girth.

Date of infestation	Approx. interval after treatment (weeks)	Treatment	No. of mealybugs (approx.)				Approximate % of mealybugs established
			Used for infestation	Remaining on the twigs and cones	Leaving the twigs and cones	On the trees on date of examination	
21 Oct. 1950	2	Control	1225	39	1186	469	39·5
		Treated	1225	12	1213	0	0
28 Oct.	3	Control	1300	95	1205	717	59·5
		Treated	1300	60	1240	20	1·6
4 Nov.	4	Control	1314	91	1223	471	38·5
		Treated	1314	9	1305	11	0·8
11 Nov.	5	Control	1500	36	1464	514	35·1
		Treated	1500	4	1492	21	1·4
17 Nov.	6	Control	1500	234	1266	571	45·1
		Treated	1500	301	1199	355	29·6
21 Nov.	7	Control	1500	54	1446	647	44·7
		Treated	1500	164	1336	654	49·0
28 Nov.	8	Control	1500	14	1486	168	11·3
		Treated	1500	5	1495	94	6·3

The plants were examined between 9 and 13 days after each infestation.

(ii) The trees were watered with dimefox at the rate of 1·6 gm. active material per in. of girth, which ranged from 6·5 to 8·5 in. Six trees were treated and another six left as controls. The method was that used in the previous experiment. The results are shown in Table XXIV; the trees evidently remained toxic for about seven weeks after treatment.

TABLE XXIV.

Persistence of dimefox at 1·6 gm. per in. of girth.

Date of infestation	Approx. interval after treatment (weeks)	Treatment	No. of mealybugs (approx.)				Approximate % of mealybugs established
			Used for infestation	Remaining on the twigs	Leaving the twigs	On the trees on date of examination	
12 Jan. 1951	5	Control Treated	1500 1500	51 47	1449 1453	505 18	34·9 1·2
19 Jan.	6	Control Treated	1500 1500	120 39	1380 1461	899 56	65·1 3·8
24 Jan.	7	Control Treated	1500 1500	78 38	1422 1462	765 91	53·7 6·2
2 Feb.	8	Control Treated	1500 1500	86 113	1414 1387	882 656	62·4 47·3
9 Feb.	9	Control Treated	1500 1500	52 91	1448 1409	1175 632	81·1 44·9

The plants were examined about 10 days after each infestation.

(iii) The trees were treated with dimefox at the dose prescribed by the girth—weight correlation (fig. 1). The girth of the treated trees ranged from 11½ to 26 in. Six treated trees and six controls were used for each infestation. The results are shown in Table XXV.

TABLE XXV.

Persistence of dimefox at the dosages based on the girth—weight correlation.

Date of infestation	Approx. interval after treatment (weeks)	Treatment	No. of mealybugs (approx.)				Approximate % of mealybugs established
			Used for infestation	Remaining on the twigs	Leaving the twigs	On the trees on date of examination	
12 Oct. 1951	5	Control Treated	1500 1500	154 205	1346 1295	238 25	17·7 1·9
19 Oct.	6	Control Treated	1500 1500	54 135	1446 1365	190 35	13·1 2·6
26 Oct.	7	Control Treated	1500 1500	70 62	1430 1438	544 88	38·0 6·1
2 Nov.	8	Control Treated	1500 1500	46 96	1454 1404	436 468	30·0 33·3
9 Nov.	9	Control Treated	1500 1500	56 58	1444 1442	596 407	41·3 28·2

The plants were examined 10 days after each infestation.

The trees treated by the dosages based on the girth—weight correlation remained toxic to mealybugs for about seven weeks.

As the insecticidal effect of one treatment, based on the girth—weight correlation, is effective at least seven weeks, re-treatment at eight-week intervals would maintain good control of mealybugs. When considering the virus control aspect, the number of re-treatments required depends on the time between the infection of a tree and the appearance of symptoms. This period is now known to vary for different strains, but in no case has the length of the symptomless period been clearly defined.

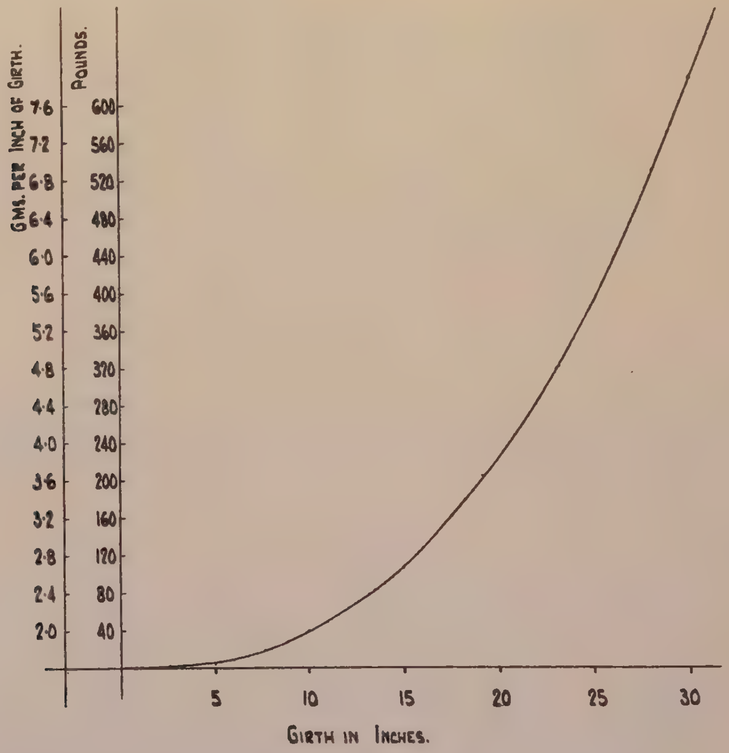


Fig. 1.—Relationship between weight of aerial part of cacao tree (in lb.), required dosage of dimefox (gm. per in. of girth) and girth of tree (in.).

(e) *Point of application of the solution in relation to the tree.*

It was mentioned earlier that in all preliminary investigations with the four insecticides, and in the detailed research programme with dimefox, the solution was poured into a slight depression round the base of the trunk.

Two experiments were carried out to find whether the application of the chemical at the base of the trunk was more efficient than applying it at different distances from the tree.

In the first experiment, the following three methods were compared:—

(i) Application at four equidistant points, each 1 ft. from the trunk.

(ii) Application to a circular depression round the trunk, at a distance of 1 ft.

(iii) Application to a circular depression round the trunk, at a distance of 2 ft.

Sixteen trees were used for each method, and a 5 per cent. solution of dimefox. Eight of each 16 trees received 0·6 gm., and the remaining eight 1·0 gm. dimefox per in. of girth. A further 12 trees were left untreated. The results are shown in Table XXVI, and it can be seen that when the solution was applied at four different points, it was not particularly effective, but it was better than when applied to a continuous circular depression at the same distance from the trunk. The average girth for each treatment ranged from 9·2 to 11·4 in.

TABLE XXVI.

The effect of the point of application of dimefox on the reduction of population.

Amount of active material per in. of girth (gm.)	Application	No. of mealybugs in 80 colonies		Population as % of that before treatment
		Before treatment	6 weeks after treatment	
0·6	Four points	922	178	19·3
	1 ft. circle	737	172	23·3
	2 ft. circle	1398	557	39·8
1	Four points	1125	154	13·5
	1 ft. circle	666	210	31·5
	2 ft. circle	704	223	31·5
Control	Untreated (120 colonies)	2441	2240	—

Total rainfall during the experiment, 7·45 in.

The second experiment was conducted to compare the application at four points with the original method of pouring the chemical directly round the trunk. For each method, eight trees, with an average girth of 11 in., were watered with a 5 per cent. solution of dimefox at the rate of 0·8 gm. per in. of girth. Four trees remained untreated. The results are shown in Table XXVII and indicate that the original method was the better. This may be attributed to the high volatility of dimefox; when it is poured directly round the trunk, the surface exposed to evaporation is smaller than when the solution is applied in a larger circle round the trunk.

TABLE XXVII.

Comparison between applying dimefox at four points and round the trunk.

Amount of active material per in. of girth (gm.)	Application	No. of mealybugs in 80 colonies		Population as % of that before treatment
		Before treatment	6 weeks after treatment	
0·8	Four points	1214	123	10·1
0·8	Round the trunk	1431	6	0·4
Control	Untreated (40 colonies)	618	581	—

Total rainfall during the experiment, 3·66 in.

Factors that might affect control.

(a) *Rain*

The eleven-year mean annual rainfall (1938–48) at Tafo, Gold Coast, is 62 in. This is a comparatively high figure, especially in view of the fact that there are considerable dry periods during the year. Moreover, there are torrential downpours, lasting only a few hours, during which as much as 2 in. rain may be recorded.

This type of rainfall might affect the soil treatment in two ways. It could be detrimental by reducing the concentration of dimefox, or by causing excessive leaching away from the region of absorbent roots. The first point was investigated by applying a 5 per cent. solution of dimefox at the rate of 1·2 gm. per in. of girth to 24 trees of approximately the same girth. Twelve of the trees received, in addition, a daily application of two litres of water, commencing immediately after the application of the insecticide, and continuing for six weeks. The remaining trees received no such application. The results of the experiment at the end of six weeks are shown in Table XXVIII and clearly indicate that under drought conditions there was no apparent detrimental effect if a fairly large quantity of water was applied to each tree.

TABLE XXVIII.

The effect of dilution of dimefox on the reduction of population.

Treatment	No. of mealybugs in 120 colonies (10 per tree)		Population as % of that before treatment
	Before treatment	After treatment	
No water	1590	112	7
Watered	1714	61	3·6
Control	697	755	—

Total rainfall during the experiment, 0·76 in.

In the second experiment, seven trees received 1·0 gm. dimefox per in. of girth, applied in 50 per cent. solution. A further seven trees received 1·0 gm. dimefox per in. of girth, applied in a 1 per cent. solution. All 14 trees received, in addition, 4 litres of water every other day. The results of the experiment after six weeks are shown in Table XXIX, and it can be seen that there is no significant difference between a solution of high or low concentration.

TABLE XXIX.

Comparison of high and low concentrations of dimefox.

Concentration %	No. of mealybugs in 70 colonies (10 per tree)		Population as % of that before treatment
	Before treatment	After treatment	
50	909	17	1·9
1	1083	57	5·3
Control	468	464	—

Total rainfall during the experiment, 3·22 in.

A further experiment, using a capsule method of applying dimefox, illustrates the effect of rain on the treatment during the rainy season. This experiment started on 16th October 1951. During the two previous weeks, a total rainfall of 9·43 in. had been recorded, of which 4·26 in. fell on 14th October. The soil was, therefore, completely saturated with water. Forty-seven trees were treated with a 50 per cent. solution of dimefox contained in capsules, and another 47 with a 5 per cent. solution applied in liquid form. Dosages were given according to the girth—weight correlation (fig. 1). Five trees for each treatment and three controls were cut down at random before the application, and the same number after six weeks. Results are shown in Table XXX. The heavy rain seems to have slightly reduced the percentage reduction of population, more particularly when the liquid form of application was used.

TABLE XXX.

Application of dimefox in capsules and as a free liquid.

Treatment	No. of mealybugs on 5 trees before treatment	No. of mealybugs on 5 trees after treatment	Population as % of that before treatment
Capsules	13183	143	1·1
Liquid	13183	476	3·6
Control (3 trees) ..	5966	7285	—

Total rainfall during the experiment, 9·13 in.

It is reckoned that 1 in. of rain on one acre of land weighs about 100 tons. Assuming that the average number of cacao trees per acre is 600, with an average girth of 17 in., the amount of dimefox applied per acre per application will be of the order of 31·6 kg. or about 0·0316 tons. This will mean that the concentration of dimefox will fall from 50 per cent., the recommended concentration, to approximately 0·032 per cent. with one in. of rain. The average monthly rainfall at Tafo is in the range of 5·2 in., or about 10·4 in. in the eight-week interval between treatments. This would still further lower the concentration to about 0·003 per cent., which might reduce the efficiency of the treatment. It can be seen from Table XXX, however, that with a total rainfall of 9·13 in. in six weeks, the percentage reduction in population was only slightly decreased.

(b) *Leaching*

An experiment was carried out to investigate the possibility of reducing the loss of dimefox through leaching by applying it in two half-doses at an interval of two weeks, as compared with a single full dose, using 0·8 cc. active material per in. of girth. Eight trees were taken for each treatment and four for control. Total rainfall during the six weeks was 3·6 in.

The difference was not very large: the trees that received the half-dose twice gave 97·3 per cent. reduction in mealybugs after six weeks, while the single application gave 98·8 per cent. The population of mealybugs on the control trees remained almost constant.

Further observations on the part played by leaching were made on a plot of cacao at Atukrum of about 13 acres (containing some 8,600 trees), which was treated with dimefox nine times, at approximately eight-week intervals, during the period 13th June 1952 to 19th September 1953, at a dose calculated from the girth—weight correlation. Some 360 kg. active ingredient was used per treatment. The ground slanted towards a small stream of running water, and some trees were right on the edge of the stream. During heavy rains, a small surface side stream made its appearance and ran into the main stream.

At about fortnightly intervals, samples of water were taken from the main stream just downstream of the site, and also from the side stream as it entered the main one. The samples were air-freighted to Cambridge for analysis by Mr. K. Gardner. About 200 separate determinations were made.

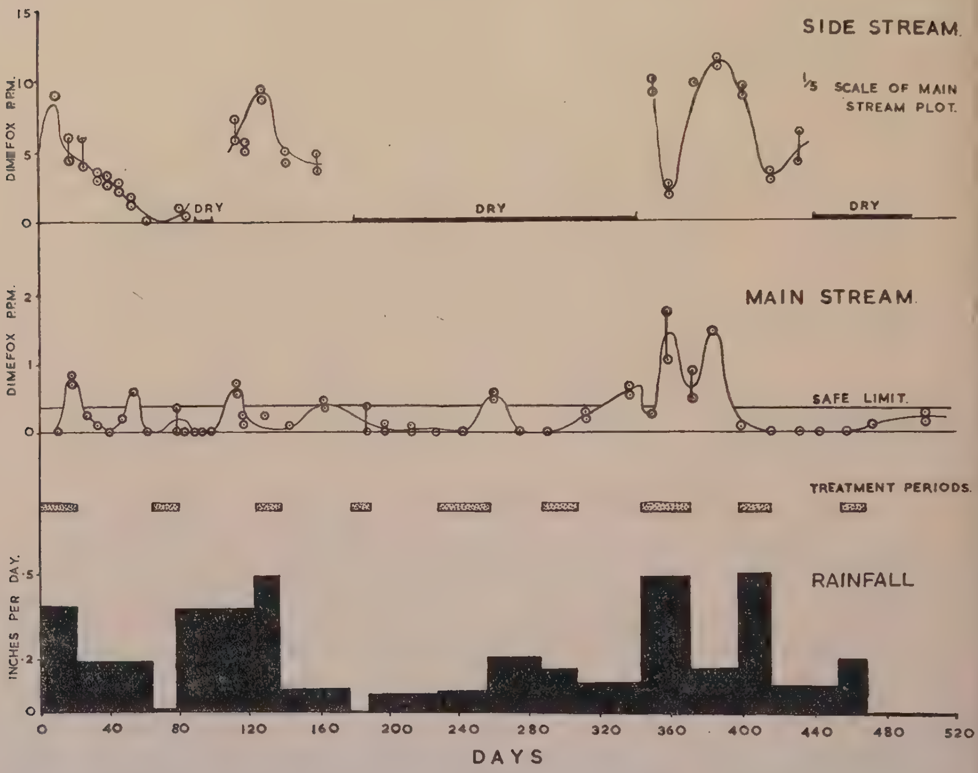


Fig. 2.—Graph showing concentration of dimefox in main stream and side stream flowing through plot of cacao trees treated with dimefox during the periods shown, and daily rainfall, Atukrum, Gold Coast, 13th June 1952–25th Sept. 1953.

The results are represented in fig. 2, showing the mean rainfall (total for the period of treatment and periods between treatment), and the concentration of dimefox in parts per million in the main stream below the site and the side stream. The control figures, for the main stream just above the site, are not shown on the graph. The graph also records the period of treatment and indicates when the side stream was not flowing.

The following points are demonstrated:—

(i) The small side stream appeared only in wet weather; it contained a much higher quantity of dimefox and responded much more quickly than the main stream. When it started to flow again after a dry period, it contained dimefox irrespective of the time when the soil was treated.

(ii) The main stream figures were much lower. The average of all figures over the whole period is 0·22 p.p.m.

(iii) The highest figures in the main stream appeared when rainfall started again after long dry periods; presumably an accumulation of dimefox in the soil was flushed out.

The control of mealybugs on this plot was satisfactory, and it seems likely that dimefox was retained in the soil in such quantities as to be effective before being leached by rain.

(c) *The uptake of dimefox by defoliated trees.*

Most of the trees attacked by swollen-shoot or Capsid bugs have a very small number of leaves, and it was thought that this might decrease uptake of solutions from the soil and reduce efficiency.

All the leaves were cut off eight trees of equal girth. The trees were then watered with 0·8 gm. dimefox per in. of girth. Another eight similar trees, from which the leaves were not cut off, received a similar application. The results six weeks after treatment were as shown in Table XXXI.

TABLE XXXI.

Application of dimefox to trees after defoliation.

Treatment	No. of mealybugs in 80 colonies (10 per tree)		Population as % of that before treatment
	Before treatment	After treatment	
Without leaves ..	977	3	0·3
With leaves ..	1088	183	16·8

Total rainfall during the experiment, 8·06 in.

It can be seen that defoliating the trees did not lessen the reduction of mealybugs.

Effect of control measures on beneficial insects.

(a) *Pollinating insects.*

Posnette (1950) found that the insects responsible for much of the cross-pollination of cacao in the Gold Coast are the Ceratopogonid flies, *Forcipomyia ingrami* Carter, *F. ashantii* Ingram & Macfie, and *Lasiohelea litoraurea* Ingram & Macfie.

The following experiment was carried out to determine the effect of the treatment on the main pollinating insects.

Thirteen days after treatment, in the large-scale experiment (Table XVII) all set and open flowers were removed from flower clusters on both treated and untreated plots. In each plot, 500 clusters were then marked, and re-examined after 14 days. On the untreated plot, 117 flowers had set as opposed to 90 on the treated. These figures are not appreciably different, and it was concluded that the treatment had had no serious effect on the pollinating insects. Since the date of this investigation, large numbers of trees have been treated and the harvesting figures support the assumption recorded above.

(b) *Parasites and predators.*

In the two large-scale field trials, involving together over 1,000 trees, that were described earlier (Tables XVII and XX), records were taken of the number of parasites and predators found in mealybug colonies before and after the application of dimefox. These records are combined in Table XXXII, and show the following points:—

(1) Cecidomyiid larvae, which are external parasites, disappeared completely when the mealybug population was greatly reduced.

(2) Larvae of the Coccinellid *Scymnus*, another external parasite, were also considerably reduced in numbers.

(3) The predatory spider, *Withius subruber* Simon, increased considerably in numbers.

It is suggested that as the mealybugs disappeared, so did the external parasites, and that as *W. subruber* is not only a predator but also a scavenger, the débris of dead mealybugs accumulated prior to removal encouraged its increase.

TABLE XXXII.

The effect of dimefox soil treatment on parasites and predators.

Parasite or predator	Experiment 1		Experiment 2	
	Before treatment	After treatment	Before treatment	After treatment
Cecidomyiid larvae	46	0	3	0
Scymnus larvae	80	9	107	2
Withius subruber	2	63	0	42

Toxicity considerations.

(a) *In the field.*

During the application of dimefox, whether in liquid or capsule form, certain precautions had to be taken to guard against its fumigant and contact toxicity. Operators were fully protected by wearing gas masks, protective clothing and rubber gloves. The utmost cleanliness was strictly observed.

At first, the required amount of liquid was measured by graduated cylinders, but a method was later devised whereby the danger of handling the chemical was minimised. A large hypodermic syringe with a rubber tube attached to it was used to draw the required amount of dimefox from its container. The outlet of the syringe had a small two-way tap, on turning which and pulling the piston, the required amount of liquid was drawn into the syringe; by turning the tap the other way, the connection to the container was closed and on pushing the piston the dimefox was expelled from the outlet of the syringe.

(b) *Toxic residues in cacao beans and pods.*

In order to determine the residual insecticide which was still present in the pods at harvest time, a sufficiently sensitive method had to be worked out. This was done by Dr. D. F. Heath and Mr. K. Gardner and based on the principle of distilling the residual dimefox with a refined mineral oil as a carrier. The method, which will be published in full elsewhere, was first of all checked by the use of radioactive dimefox, and it was found that the dimefox was so rapidly decomposed in the cacao beans that, in order to have sufficient dimefox in the living beans to check the method of analysis, it was necessary to cut immature pods and allow them to take up a water solution of dimefox through the cut stalk. The method, which was checked by the Toxicology Research Unit of the Medical Research Council, was found to be sensitive to 0·02 parts of dimefox per million parts of cacao beans.

Samples of cacao pods at different stages of maturity, ripe (yellowish/brown) and immature (green), were collected from trees treated with dimefox at the normal rate (fig. 1) and also at triple that strength, and sent for analysis to the Toxicology Research Unit, Medical Research Council, and also to Mr. K. Gardner. Sun-dried unfermented beans were also sent that had been harvested 19 and 38 days after the 1st, 6 weeks after the 2nd, 5½ and 6 weeks after the 3rd and 3 weeks after the 4th treatment from a plot at Tafo treated four times with dimefox applied to the soil at the girth—weight rates (fig. 1).

It was found that in no case was there any detectable residue of dimefox. Feeding trials were also carried out with treated, unfermented, sun-dried beans, and no residue of dimefox could be found.

(c) *Effect on water supplies.*

Dr. E. F. Edson examined the figures obtained from the analysis of about 200 samples of water (fig. 2) taken at about fortnightly intervals from the water stream previously described (p. 698), which was treated by soil application nine times at eight-week intervals at the rate prescribed in fig. 1 and reported as follows:—

"No direct practical evidence exists on the maximum permissible quantities of dimefox in human drinking water supplies, but an estimate can be made by the following reasonings:—

(i) Experiments with animal species consistently show that all species tested have been able to withstand a daily intake of 1/100th to 1/500th of the acute LD 50 dose of an organic phosphorus compound such as dimefox without the production of any deleterious effect and without even any response in the most sensitive cholinesterase enzyme. It is only at about 1/10th to 1/20th LD 50 dose daily that any effects are recognisable, *i.e.*, there is a good factor of individual safety at 1/100th to 1/500th LD 50 dose daily.

(ii) For dimefox, 1/100th of the acute LD 50 dose, for a man weighing 50 kg., would be approximately 0·5 mg. If a man consumes one litre of the water per day, a concentration of 0·5 p.p.m. dimefox would produce a daily dose of 0·5 mg. dimefox.

(iii) In order to allow for the occasional individual who may be in a slightly weaker state of health, or who drinks more than one litre of the water regularly, it is recommended that the value be reduced from 0·5 p.p.m. down to 0·3 p.p.m.

(iv) A steady and uniform dimefox concentration in drinking water is most unlikely to arise, and fluctuations are bound to occur. Provided that the *average concentration* does not exceed 0·3 p.p.m., periodic increases up to 1 or even 1·5 p.p.m. may be regarded as of no significance for public health.

(v) The above calculations are believed to represent a good factor of safety. The first indication of lack of safety at these levels, unlikely as this may be, would not consist of illness, but of a recognisable change in the blood cholinesterase enzyme. It may be of value to investigate this in persons who have regularly consumed the water for a period of several months, as an absolute confirmation of safety in practice.

(vi) A further safety factor has been introduced above in deliberately using a very low value for the LD 50 of dimefox.

(vii) There are no conceivable hazards from the use of such water for personal or domestic washing purposes."

Trunk Implantation Experiments.

General experiments.

The application of dimefox to the soil, although very efficient in killing mealybugs, was found to be expensive, as the trees required comparatively large quantities. Attempts were made to reduce costs by introducing systemic insecticides directly into the trunks of cacao trees, as it appeared that results similar to those obtained with the soil application method would be achieved with much smaller quantities.

Paraoxon, parathion, schradan and dimefox were introduced into the trunk through a hole $\frac{7}{8}$th in. in diameter and 1 ft. above the soil, drilled by a brace and bit and slanting downwards at an angle of about 45° to the trunk. The hole held about 10 cc. and it was closed by a piece of cut branch or by some dry cacao leaves, which are leathery and can be rolled into a stopper.

It was noticed that most of the chemicals poured into the holes were absorbed in a few hours. After about a week, the holes became full of water which exuded into them. In an attempt to reduce this, small plugs of cacao branches were driven hard into the holes.

In the preliminary experiment, four trees, with an average girth of 14 in., were used for each treatment, 10 cc. of solution being introduced into each hole. Four untreated trees were used as controls. The results are shown in Table XXXIII.

TABLE XXXIII.

Trunk implantation using paraoxon, parathion, schradan and dimefox.

Material	Concentration %	Active material per tree (gm.)	No. of mealybugs alive in 40 colonies (10 per tree) after			Population (as % of that on the controls) after		
			1 week	2 weeks	3 weeks	1 week	2 weeks	3 weeks
Paraoxon	25	2·5	366	822	575	79·9	>100	97·8
	20	2·0	420	556	459	91·7	70·4	78·1
	10	1·0	420	571	448	91·7	72·3	76·3
	5	0·5	452	554	456	98·7	70·1	77·6
Parathion	20	2·0	333	699	381	72·7	88·5	64·8
	15	1·5	412	686	428	90·0	76·7	72·2
	10	1·0	396	586	416	86·5	74·4	70·7
	5	0·5	454	578	424	99·1	73·2	72·1
Schradan	44	4·4	516	651	536	>100	81·4	91·2
	30	3·0	448	503	599	97·8	63·4	>100
	20	2·0	322	423	526	70·3	53·5	89·5
	10	1·0	334	785	550	72·9	99·4	93·5
Dimefox	20	2·0	76	130	90	16·6	16·5	15·3
	15	1·5	75	31	147	16·4	3·9	25·0
	10	1·0	246	81	342	53·7	10·3	58·2
	5	0·5	342	251	592	74·7	31·8	>100
Control	—	—	458	790	588	—	—	—

It could be seen, from the preceding table, that dimefox gave the best results, and it was, therefore, decided to concentrate on this and try to improve its efficiency by increasing the amount applied. The results of experiments using 10 cc. per tree at concentrations of 25–40 per cent. active material, showed that whereas, on examination after treatment, some branches gave low counts of live mealybugs, others yielded correspondingly high figures. This variability appeared to be related to the position of the bore hole, and an experiment was designed to investigate it.

A tree was selected having branches radiating in all directions from about the same point on the trunk. It was injected on 31st May 1950, with 11 gm. of

20 per cent. solution of dimefox. The branches were numbered and from each of them, both before and after treatment, 13 colonies were taken for examination (fig. 3). After 18 days, the results were as shown in Table XXXIV.

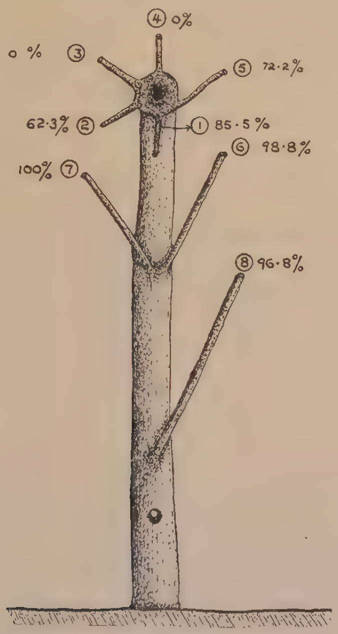


Fig. 3.—Semi-diagrammatic representation of cacao tree, showing position of principal branches in relation to injection hole (near base of trunk) and the percentage reduction of their original mealybug populations following injection of the trunk with dimefox.

As can be seen from Table XXXIV and fig. 3, the greatest reduction of mealybugs occurred on those branches directly above the bore hole, the smallest reduction being found on branches originating from a point on the trunk opposite to the bore hole.

TABLE XXXIV.

Lack of uniformity in the response to dimefox implanted in a single hole in the trunk.

Branch no.	No. of mealybugs alive in 13 colonies before treatment	No. of mealybugs alive in 13 colonies after treatment	Population as % of that before treatment	% reduction of original population
1	180	26	14·5	85·5
2	263	99	37·8	62·2
3	174	195	>100	0
4	88	199	>100	0
5	709	195	27·5	72·5
6	172	2	1·2	98·8
7	169	0	0	100·0
8	63	2	3·2	96·8

Upward and downward translocation in the trunk implantation method.

Translocation of the insecticide was investigated by counting, on 28th May 1950, the number of live mealybugs in 20 colonies on branches originating from the stem above and below the bore holes on trees that had been injected three weeks previously with 10 cc. of different concentrations of dimefox. Results are shown in Table XXXV, and it can be seen that when dimefox is injected into the tree it is translocated upwards, but not downwards.

TABLE XXXV.

Trunk implantation using higher concentrations of dimefox.

Concentration of dimefox %	No. of mealybugs in 20 colonies on branches above the injection hole	No. of mealybugs in 20 colonies on branches below the injection hole
20	65	400
15	16	357
10	40	322

Increasing the efficiency of the trunk implantation method.

In the experiments carried out previously, only one hole per tree was used. This seemed insufficient to give even distribution of dimefox to all branches of the tree, and the following experiments were made to investigate (a) the minimum number of holes required per tree to ensure uniform distribution of dimefox, (b) the location of the holes, and (c) the minimum effective dose per tree.

(a) *3 holes per tree, 3 ft. above soil level.*

The holes were $\frac{5}{8}$th in. in diameter and the amount of dimefox used (in 50 per cent. concentration) was $\frac{1}{4}$, $\frac{1}{8}$ or $\frac{1}{16}$th the dosage prescribed by the girth—weight correlation for soil application. The dose was divided equally

TABLE XXXVI.

Trunk implantation using 3 holes per tree, 3 ft. above soil level.

		No. of mealybugs alive in 100 colonies (20 per tree)				
Treatment	Dose*	Before treatment	2 weeks after treatment	Population as % of that before treatment	4 weeks after treatment	Population as % of that before treatment
Trunk implantation	$\frac{1}{4}$	1074	3	0·3	0	0
	$\frac{1}{8}$	1068	317	29·7	10	0·9
	$\frac{1}{16}$	962	420	43·6	154	16·0
Soil treatment	$\frac{1}{4}$	1289	275	21·4	192	4·1
	$\frac{1}{8}$	980	635	64·9	526	53·7
	$\frac{1}{16}$	1305	716	54·9	568	43·5
Control		1382	904	—	1194	—

* As fraction of that prescribed by the girth—weight correlation.

between the holes, being delivered by a hypodermic syringe, and the holes sealed by driving small wooden plugs into them. The implantation method was compared with soil treatment, using the same dosages. Five trees were used for each treatment and for control. Twenty colonies were taken from each tree before and after treatment, and the number of mealybugs in each was recorded. No pods were present on the trees during treatment. The results are shown in Table XXXVI.

The trunk implantation method gave very good results, using $\frac{1}{4}$ the dose of the soil-application rate.

(b) *3 holes per tree, 2 in. above soil level.*

The holes were $\frac{5}{16}$th in. in diameter and 3·5 in. deep and the amounts of dimefox used were $\frac{1}{8}$, $\frac{1}{12}$, $\frac{1}{16}$, $\frac{1}{20}$ and $\frac{1}{24}$th of the dosages prescribed by the girth—weight correlation for soil application. The holes were closed with wooden plugs $\frac{1}{2}$ in. long and then covered with " Pentol " wax, which is pliable and does not flake. Ten trees were taken for each treatment, ranging from 7 to 16 in. in girth. The results are shown in Table XXXVII.

TABLE XXXVII.

Trunk implantation using 3 holes per tree, 2 in. above soil level.

Dose*	No. of mealybugs alive in 200 colonies (20 per tree)					Total mealybugs found on 10 trees, 6 weeks after treatment
	Before treatment	4 weeks after treatment	Population as % of that before treatment	6 weeks after treatment	Population as % of that before treatment	
$\frac{1}{8}$	4054	26	0·6	28	0·7	78
$\frac{1}{12}$	3104	526	16·9	183	5·9	932
$\frac{1}{16}$	3198	80	2·5	106	3·3	228
$\frac{1}{20}$	5214	152	2·9	176	3·4	476
$\frac{1}{24}$	4220	61	1·4	105	2·5	270
Control	4176	4385	>100	4461	>100	—

* As fraction of that prescribed by the girth—weight correlation.

In the above experiment, it was noticed that the live mealybugs were found after treatment on the big trees, and on one or two branches of the trees while the remaining parts were free. This suggested that the distribution of dimefox over the whole tree required still further improvement.

(c) *4–5 holes per tree at soil level.*

The holes were $\frac{5}{16}$th in. in diameter and 3·5 in. deep, bored at soil level, and four were used for trees below 25 in. girth and five for larger trees. The amounts of dimefox were $\frac{1}{5}$, $\frac{1}{10}$, $\frac{1}{15}$ and $\frac{1}{20}$th of the normal dose for soil treatment. Ten trees were used for each treatment, ranging from 6–26 in. girth, and another ten trees for control. The results are shown in Table XXXVIII.

Although the results of this experiment were an improvement on the others, yet the seven mealybugs found alive after the first treatment, which were on a 26-in. girth tree, the largest one in the experiment, suggested that the dosage was not yet correctly adjusted.

TABLE XXXVIII.

Trunk implantation using 4–5 holes per tree at soil level.

	No. of mealybugs in 200 colonies (20 per tree)					
Dose*	Before treatment	4 weeks after treatment	Population as % of that before treatment	5 weeks after treatment	Population as % of that before treatment	Total mealybugs found on 10 trees 5 weeks after treatment
$\frac{1}{5}$	2901	11	0·4	1	0·3	7
$\frac{1}{10}$	2744	2	0·1	14	0·5	70
$\frac{1}{15}$	2047	20	0·9	38	1·8	138
$\frac{1}{20}$	2374	132	5·5	176	7·4	795
Control	2166	—	—	2413	—	—

* As fraction of that prescribed by the girth—weight correlation.

If the trees which gave an appreciable control of mealybugs in the above experiment are segregated into groups according to the amount of dimefox used in relation to their weight, the result is as shown in Table XXXIX.

It can be seen that the best results were obtained when using approximately 1 gm. of active dimefox per 9–14 lb. (4·1–6·4 kg.) of the aerial part of the trees. That is roughly of the order of 160–250 p.p.m.

TABLE XXXIX.

Effectiveness of implanted dimefox in relation to ratio of tree-weight to dosage.

No. of trees	Range of :—				No. of mealybugs on all trees (20 colonies per tree)		Population as % of that before treatment	Total no. of mealybugs on all trees after treatment	No. per tree
	Girth (in.)	Weight of tree (lb.)	Amount of dimefox used (gm.)	Ratio weight of tree to dosage dimefox (lb./gm.)	Before treatment	5 weeks after treatment			
10	9–26·5	30–457	3·4–33	9–14	2691	1	0·03	7	0·7
5	7–11	15–49	0·8–2·4	19–20	1058	7	0·7	7	1·4
7	10–25	39–393	1·4–13·8	28–29	2122	14	0·7	56	8
11	9–19	30–196	0·9–4·8	33–41	2267	176	7·7	758	69

In using, in the trunk-implantation method, a fraction of the doses prescribed by the girth—weight correlation (fig. 1) for soil application, it seems that small trees were overdosed while big ones were underdosed (Table XL).

In the trunk-implantation method, the dosages should, therefore, be calculated in parts by weight of dimefox per million parts by weight of the trees, and not as a fraction of the soil-application rates, for when applying dimefox to the soil, the amount required to render a given weight of a tree toxic to mealybugs, varied according to the tree size (see Table XL). A similar variation does not seem to be required when using the trunk-implantation technique. This may be due to the fact that the chemical is placed directly into the tree, and no factor of soil absorption, leaching or evaporation from the soil is present. The loss of chemical in the soil-treatment method seems to be relatively greater in proportion to the size for smaller trees, for these require a relatively bigger dosage per unit of weight.

As this method of treatment seemed promising, further detailed experiments were carried out jointly with the Cacao Research Institute, the results of which will be the subject of a separate publication.

TABLE XL.

Amounts of dimefox given in relation to the weight of cacao trees in the soil treatment method.

Tree girth (in.)	Weight (lb.)	Amount of dimefox used in soil treatment (gm.)	Wt. of tree (in lb.) per gm. dimefox
5	6·7	8	0·84
10	38·8	20	1·9
15	108	40·5	2·7
20	224	77	2·9

Conclusions.

From the experience so far obtained, it seems that soil treatment with dimefox is very efficient in reducing the cacao mealybug population to a very low level. The method is very simple, does not need machinery and can be carried out quickly: five trained Africans can treat about 1,500 trees in five hours. It has no apparent detrimental effect on the health of the plant: in a 13-acre plot in which the trees were treated nine times at eight-week intervals (p. 697), the yield was found to be normal or slightly above it.

On the other hand, the saving in the quantities of insecticide by the use of the trunk-implantation method is likely to be considerable, as the insecticide is placed directly into the tree, thus involving no wastage of chemical by leaching, etc., as compared with the soil treatment. The method is very slow, but it could be made quicker if mechanised.

As dimefox is very poisonous, the treatments should only be carried out by trained men under technical supervision.

Summary.

The swollen-shoot virus of cacao is transmitted in the Gold Coast by mealybugs, of which *Pseudococcus njalensis* Laing is the most important, and these are tended by ants of the genus *Crematogaster*, which build carton tents over the colonies, thus affording them protection against contact insecticides. An account is given of an investigation which was carried out at Tafo, Gold Coast, between 1950 and 1953, of the possibility of controlling mealybugs and thus the spread of the virus, by the use of systemic insecticides. Dimefox, schradan, paraoxon and parathion were tested, although the two last are not strictly systemic in action.

It was found that ants removed dead mealybugs from the tents, thus making it impossible to assess the effects of treatments from the numbers of live and

dead mealybugs in the colonies. Accordingly, in experiments using few trees, samples of colonies were taken at random from each, before and at intervals after treatment, the tents opened and the contents counted. In large-scale treatments, involving 250–500 trees, the area was divided into sub-plots of 50 trees, of which five from each sub-plot were cut down at random before and five after treatment and all mealybugs found on them counted. In both cases the results were expressed as the size of the population after, as a percentage of that before, treatment. The insecticides were tested as solutions sprayed on to the tree, applied to the soil at its base or introduced into a hole drilled in the trunk. Doses throughout refer to amounts of active ingredient.

The effects of all the insecticides as sprays at concentrations of up to 1·0 per cent. were unsatisfactory or inconsistent. Schradan, paraoxon and parathion, the first at 0·5 and the two latter at 1·0 gm. in 100 cc., had no pronounced effect when applied to the soil around ten-month-old seedlings growing singly in pots and artificially infested. By contrast, dimefox gave very effective initial kills at doses as low as 0·1 gm. per plant and a range of concentrations from 0·1 to 20 per cent., while doses of 0·4 gm. rendered year-old plants toxic for up to six weeks. When the four insecticides were applied at 40 gm. in 4 litres solution to trees of average size in the field, dimefox again showed marked superiority and efforts were accordingly concentrated on developing methods for its field use.

In order to relate effective dose to tree size, the latter was expressed as girth measurement one ft. above ground level and soil applications of amounts of dimefox ranging from 0·4 to 1·4 gm. per in. of girth were tested. The reductions in populations obtained at the higher rates, though substantial, were deemed insufficient and inconsistent. A further experiment was then made using 500 trees, ranging in size from 3 to 20 in. girth, in which the total mealybug populations on the ten groups of sample trees examined six weeks after treatment ranged from 0 to 4·5 per cent. of those on similar groups before treatment. Individual tree records indicated that the majority of the survivors was on the large trees (12½–20 in. girth). By applying a range of doses to further samples of trees falling into different girth-groups, a relationship was established empirically between the dose, in gm. per in. of girth, required for effective mealybug control, and tree girth, and thus with tree weight, investigations on 428 trees with girths from 5–30 in. having shown that the weight of the aerial part of the tree could be related to girth by a formula, which is given.

A test of the efficiency of the doses prescribed by this girth-weight correlation and applied as solutions containing 5 per cent. dimefox was made on a further 500 trees, of girths 3·5 to 18·5 in. On the 50 trees examined before treatment, the numbers of mealybugs found ranged from 3–5,200 per tree and totalled 42,971, while on the 50 trees examined six weeks after treatment, a total of 35 mealybugs was found, 33 trees having none and the rest from 1 to 7 each. Similar counts made at the start and end of the six-week period on samples of five trees from a similar but untreated plot yielded 3,017 and 5,969 mealybugs, respectively.

Repetition of the original treatment at different intervals on different plots indicated that two further applications at eight-week intervals kept the mealybug population at a very low level (0·6% of that originally found) for about six months, a period that was thought at the time to be the maximum for latent virus infection. On trees that received only the original treatment, the build-up of mealybugs seemed rather slow, the sizes of the populations as percentages of that before treatment being 0·08, 2·5, 9·4 and 15·5 on successive samples of 20 trees examined after 6, 12, 18 and 24 weeks, respectively. Subsidiary experiments using doses based on the girth-weight correlation demonstrated that trees remained effectively toxic (as judged by less than 10% establishment of the mealybugs with which they were artificially infested) for about seven weeks.

Subsidiary investigations showed that the effectiveness of dimefox applied to the soil was only slightly affected by heavy rain and not at all by defoliation of the trees, that no detrimental effect on pollinating insects was observed, and that the cacao beans were not rendered toxic. The water in a stream flowing through a 13-acre plot of cacao trees treated at the prescribed doses nine times at eight-week intervals showed an average concentration, just below the site, of 0·22 parts per million dimefox over the whole period. The insecticide is best applied to a depression in the soil made immediately round the base of the tree, but it is as effective when applied in sealed capsules that disintegrate when placed in the soil. Either method of application is simple and neither involves the use of heavy machinery, which is unsuitable for Gold Coast conditions.

In preliminary tests of the possibility that smaller quantities of insecticide might be needed if it was introduced into a hole drilled into the trunk, only dimefox gave encouraging results. Further experiments with this method showed that dimefox was translocated upwards only and that the greatest reduction in populations occurred on those branches directly above the hole. It was found that a more even distribution of dimefox was obtained with four holes (or five for trees of 25-in. girth or over) each $\frac{5}{16}$th in. in diameter by 3·5 in. deep, drilled at soil level. Mealybug populations remained substantially reduced (to 0·5% or less of the value before treatment) five weeks after introducing doses only $\frac{1}{10}$th of those prescribed by the girth—weight correlation for soil treatment. It appeared, however, that inoculation doses calculated by this method were excessive for small trees and inadequate for big ones, and that they should instead be calculated as a fixed fraction of the weight of the tree, a rate of 160–250 p.p.m. being the most satisfactory.

Acknowledgements.

This work was carried out by the authors whilst members of the team provided by Messrs. Pest Control Ltd. and they are indebted to the Directors of Messrs. Fisons Pest Control Limited, Bourn, Cambridge, and to the Director of the West African Cacao Research Institute, Tafo, Gold Coast, for permission to publish these results.

We also acknowledge gratefully the valuable suggestions, help and encouragement given to us by Dr. W. E. Ripper, of Pest Control Ltd.

Our thanks are due to Mr. O. W. Snow, Dr. G. S. Hartley, Dr. R. M. Greenslade and Dr. E. F. Edson, of Pest Control Ltd., for the facilities and help accorded to us, and in particular to Mr. K. Gardner, for his analysis of some 200 samples of water.

We are also obliged to the Senior Entomologist and the Agronomist of the West African Cacao Research Institute for their kind help, and to Dr. J. A. R. MacLean, Chief Chemist, who kindly carried out in his Department the analysis of the water contents of the heart- and sap-wood of cacao.

Our thanks are also due to our colleagues of the Biological, Chemical and Medical Research Departments of Pest Control Ltd., and to Mr. Osae and Mr. Owusu Kredua who ably assisted in the field and insectary work.

References.

Berkeley, G. H., Carter, W. & van Slogteren, E. (1948). Report of the Commission of Enquiry into the swollen shoot disease of cacao in the Gold Coast.—Colon. no. 236, 10 pp. London, H.M.S.O.

Box, H. E. (1945). Insect transmission of the "swollen-shoot" virus in West African cacao.—Nature, Lond., **155**, pp. 608–609.

Broatch, J. D. (1953). Cocoa production and disease control in West Africa. Part I. The progress of the Gold Coast swollen-shoot control campaign.—Rep. Cocoa Conf., 1953, pp. 76–79. London, Cocoa, Choc. Confect. Alliance.

Cotterell, G. S. (1943). Entomology.—Rep. cent. Cocoa Res. Sta. Tafo, 1938–42, pp. 46–55.

Hanna, A. D., Heatherington, W. & Judenko, E. (1952). Control of the mealybug vectors of the swollen-shoot virus by a systemic insecticide.—Nature, Lond., **169**, pp. 334–335.

Nicol, J. (1952). Systemic insecticides and the mealybug vectors of swollen-shoot virus of cacao.—Nature, Lond., **169**, p. 120.

Posnette, A. F. (1941). Swollen-shoot virus disease of cacao. (Review of research work to November 1940.)—Trop. Agriculture, **18**, pp. 87–90.

Posnette, A. F. (1950). The pollination of cacao in the Gold Coast.—J. hort. Sci., **25**, pp. 155–163.

Posnette, A. F. & Strickland, A. H. (1948). Virus diseases of cacao in West Africa. III. Technique of insect transmission.—Ann. appl. Biol., **35**, pp. 53–63.

Strickland, A. H. (1947). Coccids attacking cacao (*Theobroma cacao* L.), in West Africa, with descriptions of five new species.—Bull. ent. Res., **38**, pp. 497–523.

Strickland, A. H. (1951). The entomology of swollen-shoot of cacao. I. The insect species involved, with notes on their biology.—Bull. ent. Res., **41**, pp. 725–748.

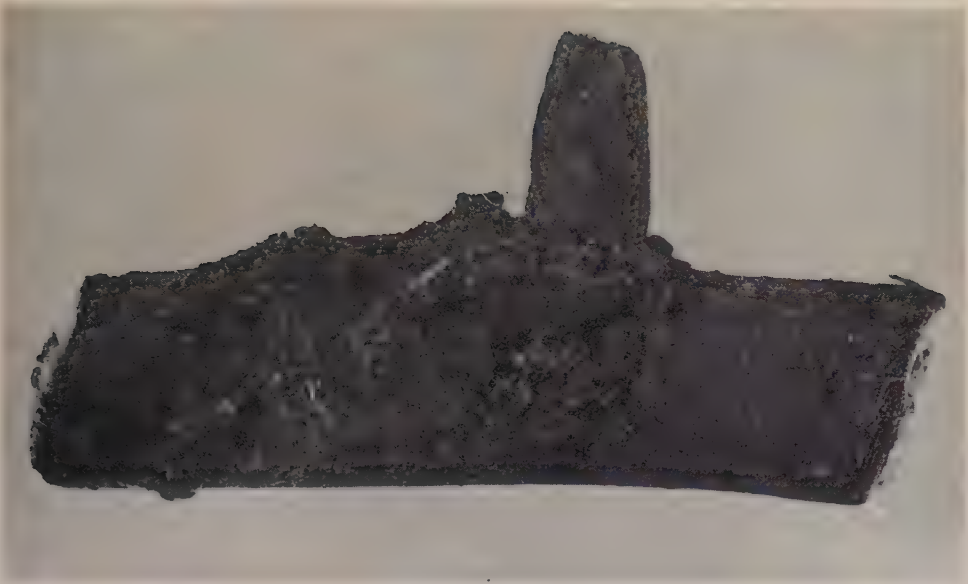


FIG. 1. Cacao twig carrying large protecting tent showing ant entrances.

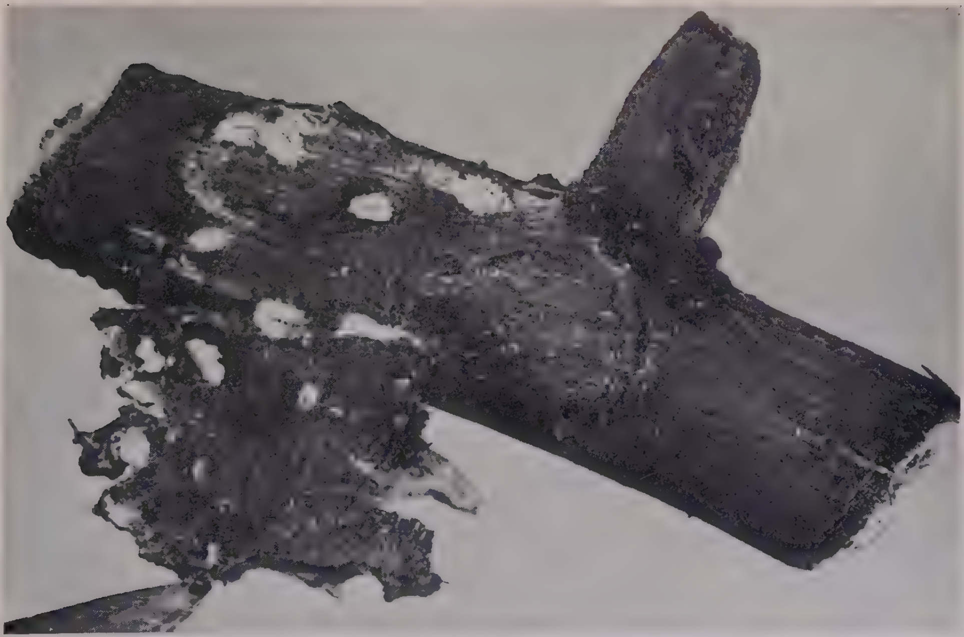


FIG. 2. Tent shown in fig. 1, opened to show the sheltered mealybugs.

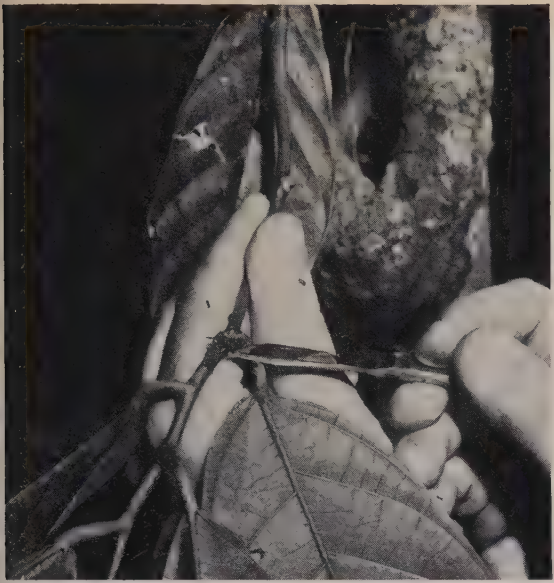


FIG. 1. Cacao twig bearing mealybug tents built by ants.

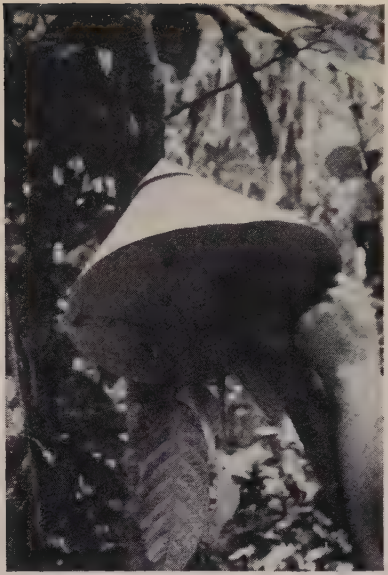


FIG. 2. Paper cones to protect mealybugs during artificial infestation.

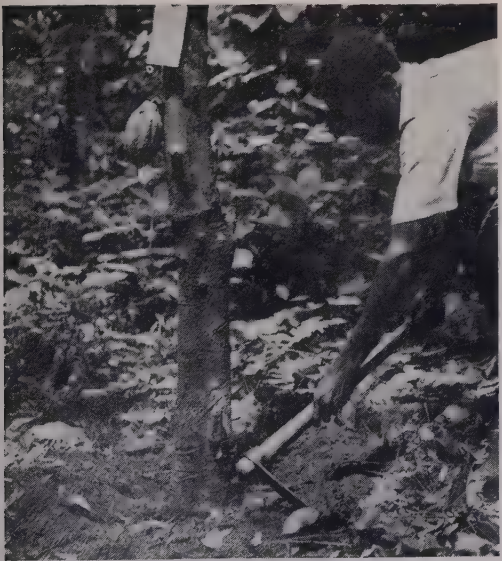


FIG. 3. Making a depression round the base of a cacao tree to receive liquid systemic insecticide.

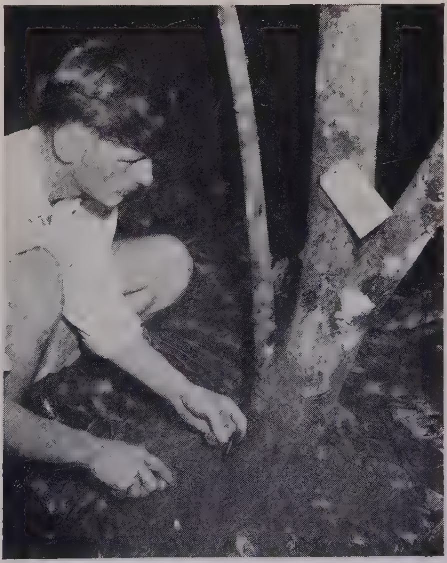


FIG. 4. Applying dimefox in a capsule at the base of a cacao tree.

STUDIES ON THE BIONOMICS OF *AËDES AEGYPTI* (L.) IN ITS NATURAL HABITATS IN A COASTAL REGION OF KENYA.*

By C. Teesdale, Ph.D.
Division of Insect-borne Diseases, Medical Dept., Kenya.

(Plate XXII.)

The epidemiology of yellow fever in East Africa has been the subject of considerable research in recent years, the work of Haddow, Lumsden, Smithburn and their co-workers in Uganda being particularly prominent; they have shown that dissemination of the disease there is almost certainly associated with a double cycle of transmission between *Aëdes* (*Stegomyia*) *africanus* (Theo.) and forest monkeys and *A.* (*S.*) *simpsoni* (Theo.) and man (Mahaffy & others, 1942; Haddow & others, 1948; Smithburn, Haddow & Lumsden, 1949). *A.* (*S.*) *aegypti* (L.), the proved vector elsewhere, did not appear to be implicated, but this species is very common along the Kenya coast and, in 1939, measures were initiated for its control there as well as along the lines of communication between Kenya and Uganda.

At the outset little was known of the bionomics of *A. aegypti* locally and it soon became evident that if eradication was to be achieved a wider knowledge of the insect's behaviour under natural conditions was essential. The present investigations were, therefore, undertaken with this objective as their primary purpose.

Part of the tabulated data from which a number of the text figures has been plotted, have been omitted from this paper. Copies of these Tables, which give details of meteorological conditions, window-trap catches, ovulation, digestion, and reduction in numbers of larvae and adults by larval control, have been deposited in the archives of the British Museum (Natural History), London, where they are available for examination by those interested.

General Description of the Area.

The investigations were carried out in three separate localities at Mombasa, Kenya, (a) on the island of Mombasa itself, (b) at the small village of Jomvu, on the mainland about eight miles west of Mombasa Island and (c) in plantations on the mainland five miles due west of the island, in a locality known as Kwa Shekh.

Only that part of the work connected with the biting-cycle was done on the island, in situations much resembling those at Kwa Shekh, a village that lies within a broken belt of coconut trees, fringing the coast (Pl. XXII, fig. 1), which varies from about half to two or three miles in width. Tree holes, discarded domestic receptacles, fallen coconuts and leaves and foot-holes in the trunks of the palms afford innumerable breeding places for *A. aegypti* and other mosquitos. All three areas are closely settled and habitations consist of rectangular Swahili-type dwellings constructed with mud walls and palm-leaf thatch which are scattered among plantations of intermixed mango, cashew-nut and coconut trees, all planted haphazardly (Pl. XXII, fig. 2). They form a rather discontinuous canopy with groups of banana plants, pineapples and cassava beneath;

---

* Approved in its original form for the Ph.D. degree of London University.

otherwise ground cover consists of low-growing indigenous bush and grass. The soil is generally sandy and porous, except in places where underlying patches of shale are exposed and in such situations shallow swamps may be formed in the rainy seasons and hold water for some months.

Being part of the coastal plain, the land is generally level, 50 to 80 ft. above sea-level, but well dissected by small ravines which are normally dry and drain steeply to the sea. At Kwa Shekh there is a small village of about three dozen houses (Pl. XXII, fig 3), but Jomvu is larger and just outside the coconut belt and, unlike Kwa Shekh, there is no shade from larger trees such as mangos and palms (Pl. XXII, fig. 4).

Mombasa is situated only four degrees south of the equator and the climate is influenced by both the north-east and south-east monsoons, the former blowing from December to March, the latter from June to September. Rainfall, which has averaged about 47 in. for the past ten years, occurs between these two periods, that is, before the new monsoon becomes established. The so-called "long" rains occur in April and May and the "short" rains in October or November. There is no marked seasonal variation in temperature, the hot season mean being 86·2°F. and the cool season 73·9°F. Daily range varies between 71°F. and 82°F. in the cool months of July and August and 77°F. and 91°F. in the hot dry months of February and March. Relative humidity is consistently high throughout the year (average of 74%) but there may be a considerable seasonal variation, figures as low as 69 per cent. often being recorded in the dry months and over 90 per cent. during the rains; variation between night and day, however, is slight. Details are shown in Tables I and II and fig. 1.

TABLE I.

Meteorological data, Mombasa. Average figures over a period of ten years.

Month	Mean max. temp. (°F.)	Mean min. temp. (°F.)	Rel. humidity (%)	Precipitation (in.)
January ..	87·8	76·1	71	1·02
February ..	89·9	77·2	69	0·66
March	90·1	78·4	72	2·56
April	89·8	77·8	73	7·32
May	83·3	74·5	81	12·65
June	83·3	73·1	76	4·53
July	82·0	71·8	77	3·84
August ..	82·3	71·4	77	2·42
September ..	83·4	72·2	76	2·55
October ..	85·7	73·9	71	3·21
November ..	88·6	75·6	71	3·91
December ..	88·6	75·8	73	2·33
Mean annual	86·3	74·8	74	47·00

TABLE II.

Mean times of sunrise and sunset monthly at Mombasa (4° 04′ S.),
East African Standard Time.

Month	Sunrise	Variation from the annual mean	Sunset	Variation from the annual mean	Hours of sunlight
January	0619 hr.	0 min.	1837 hr.	14 min.	12 hr. 18 min.
February	0628 ,,	9 ,,	1841 ,,	18 ,,	12 ,, 13 ,,
March	0628 ,,	9 ,,	1835 ,,	12 ,,	12 ,, 17 ,,
April	0622 ,,	3 ,,	1822 ,,	–1 ,,	12 ,, 00 ,,
May	0620 ,,	1 ,,	1815 ,,	–8 ,,	11 ,, 55 ,,
June	0625 ,,	6 ,,	1815 ,,	–8 ,,	11 ,, 50 ,,
July	0630 ,,	11 ,,	1822 ,,	–1 ,,	11 ,, 52 ,,
August	0628 ,,	9 ,,	1823 ,,	0 ,,	11 ,, 55 ,,
September	0616 ,,	– 3 ,,	1818 ,,	–5 ,,	12 ,, 02 ,,
October	0604 ,,	–15 ,,	1812 ,,	–9 ,,	12 ,, 08 ,,
November	0559 ,,	–21 ,,	1812 ,,	–9 ,,	12 ,, 13 ,,
December	0606 ,,	–13 ,,	1824 ,,	1 ,,	12 ,, 18 ,,

Compiled from times correct to within two minutes for any year.

Near the equator the times of sunset and sunrise may vary over a period of 30 to 40 minutes during the year although the length of day is almost constant (Haddow, 1945; Mattingly, 1949*a*, *b*; Lumsden, 1952). Conditions at Mombasa (4°, 04′ S.) would therefore be similar, and catches which started at 7 a.m. or 6 p.m. (E.A. Standard Time) would not always have been made at exactly the same time after sunrise or before sunset. The annual variation at Mombasa is actually over a period of 28 minutes.

It is considered that the nature of the catches in the present studies is such that the daily variation between the times of sunrise and sunset is unlikely to influence any deductions which may be drawn from them. All times used in these investigations are East African Standard Time.

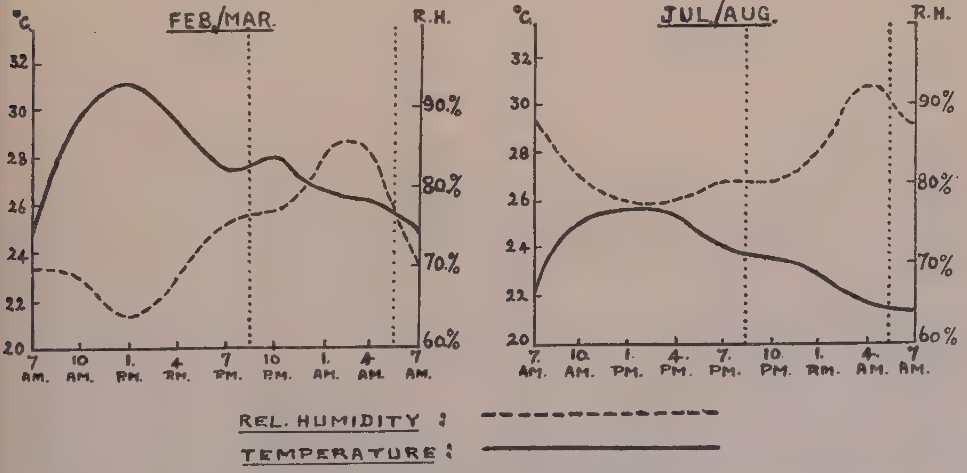


Fig. 1.—Mean daily range of temperature and relative humidity at Kwa Shekh for Feb.–Mar. and July–Aug., 1950 and 1951.
Note.—The curves lying between the dotted vertical lines are means of only five readings in Feb.–Mar. and six in July–Aug.

Larval Development.

The time required for larval development of *A. aegypti* on the Kenya coast was not known but, for considerations of control which was already in operation, based on a seven-day cycle, it was most important to be sure that it was not less than one week, since a period as short as 85 hours had been reported by Mattingly (1952) in West Africa and four days by Young (1922) in Brazil.

Conditions approximating as nearly as possible to those in nature were achieved by selecting containers found naturally infested with larvae and covering them *in situ* with wire-gauze cages until development had been completed. The covers were then removed and the containers examined frequently to see when fresh eggs were laid. (If present they were always found on the water—not on the sides of the receptacle—but females were not seen actually ovipositing.) Unfortunately, this method was fraught with difficulties, as eggs of more than one species were often found together or, when the adults emerged, they were mosquitos other than *A. aegypti*. Attempts to identify the eggs on the surface of the water with a lens were not always successful and it was feared that removing them for closer examination might vitiate the experiments.

Finally, recourse was made to eggs laid in the laboratory, batches of which, after counting, were transferred to the containers, the cages replaced and records kept of the rate of development. By this means the eggs hatched and the larvae developed in an environment chosen by a female *A. aegypti*.

TABLE III.

Development of *Aëdes aegypti* from egg to adult.

	In a house Test no.		In bush Test no.					
	1	2	1	2	3	4	5	6
No. of eggs	96	134	6	74	39	41	96	86
Conditioned or not ..	Yes	Yes	Yes	No	No	No	No	Yes
Egg to 1st-stage larva (days)	1–1½	1–2	1–2	2–4	2–4	1–3	1–3	1–2
1st to 2nd stage (days) ..	1	1	3	2	1	2	1	1
2nd to 3rd stage (days) ..	1	1	2	2	1	1	2	1
3rd to 4th stage (days) ..	1	2	2	2	2	2	1	1
4th stage to 1st pupa (days)	2	2	1	2	2	2	1	2
1st pupa to 1st adult (days)	2	2	2	3	2	2	2	1
1st pupa to last adult (days)	5	6	5	13	6	5	5	9
Egg to first adult (days) ..	8	9	11	15	11	12	10	8
Egg to last adult (days) ..	11	12	14	25	15	15	13	15
No. of adults	77	121	2	59	26	31	30	50
Per cent. emergence	80·2	90·3	33·3	79·7	66·7	75·6	31·3	58·2
No. of males	60	76	—	39	12	18	17	30
No. of females	17	45	2	20	14	13	13	20

The tests (eight in all) were completed between October 1951 and February 1952. The temperature of the water, taken thrice daily (but not at night), varied only slightly from day to day or month to month and differed very little indoors or outside. It averaged 77·9°F., 82·4°F. and 77·9°F. at 6 a.m., 2 p.m. and 6 p.m., respectively.

Conditioned eggs—those which had been kept on damp filter paper or cork for two days before being placed in water—were used for four out of the eight tests; otherwise eggs not older than twelve hours were used.

Details of the results obtained are given in Table III.

The following were the more salient points arising from the tests:—

1. Eclosion occurred more rapidly in conditioned eggs but whether conditioned or not there was no difference in the percentage of larvae which completed development.
2. There was a tendency for larvae from conditioned eggs to complete development a little sooner than those from unconditioned ones.
3. A higher percentage completed development indoors (85% compared with 57% out-of-doors).
4. The shortest period in which development was completed was eight days—both inside and outside.
5. Males predominated in the proportion 17 to 10.

The more rapid eclosion of conditioned eggs confirms the finding of Buxton & Hopkins (1927) and Shannon & Putnam (1934) as well as other workers. Young (1922), however, was of the opinion that eggs generally do not hatch if they are floating on the water surface; he considered that submergence by rain or other means is necessary first. So far as is known, the eggs in these tests were not submerged and because it was not possible to count the larvae as they hatched, it was not known whether all that did so became adults. From a total of 572 eggs, 396 (69%) adults emerged.

Cannibalism is said to occur if food supplies are short (Drake-Brockman, 1913) and this may have happened in the present tests, although the author has never witnessed it in this species.

There may be some significance in a higher proportion of larvae completing their development indoors, but there were insufficient tests to confirm this and nothing was known regarding the quality and quantity of food supplies. Whatever the nutritional values may have been, these containers can be taken as being representative of the type of breeding place normally chosen, as eggs were found in all of them. Thus eight days is probably the normal minimum period required for development on the Kenya coast.

The Proportion of Males to Females.

Opinion seems to be that, in any batch of eggs, males generally predominate (Rees, quoted by Gordon, 1922; Young, 1922; Johnson, 1937; Christophers, 1952, personal communication) but Nuttall & Shipley (1901) found the proportion equal and Gordon (1922) maintains that males are in excess only if food supplies for the larvae are favourable.

In these tests males outnumbered females in the proportion of 17 to 10, although a few more females emerged in two batches of eggs. W. H. R. Lumsden (private communication) has suggested that in the eggs the sexes may be more or less evenly balanced and that any differences found after hatching might be a result of differential mortality while in the larval state or immediately after hatching. Natural enemies might also account for a preponderance of males as it is generally considered that the development of females takes slightly longer, so that in consequence the risk of attack would be proportionately increased.

In routine hand-net captures of adult mosquitos made outside during 1943 and 1944 in different types of environment, in which the searchers used small sticks to disturb resting mosquitos in the vegetation, 2,317 males and 3,714 females were taken, and in weekly captures made throughout these investigations 81 males and 238 females were captured; but it is probable that the preponderance of females was due to hunger which enabled them to be more readily captured. It was not easy to find resting *A. aegypti*, but the commoner situations were on the underside of leaves of small bushy plants or on the extremity of twigs and leaves in shady places; not infrequently they were taken low down on tree trunks.

In the window-trap captures (p. 718), males were generally fewer than females whether they were taken going into or leaving rooms. Breeding was always taking place in these rooms and if, as these tests indicate, males outnumber females in any batch of eggs, more males should have been caught in the exit traps, unless they tend to remain indoors more than do females.

Flight and Dispersion.

As even females were often very scarce, an endeavour to step up the captures was made by establishing an artificial breeding place which would produce many adults, and alongside which catching should be done. For this purpose two large drums were let into the ground under a tree and filled with rain-water and débris to a depth of about six in.; it was not long before both drums were heavily infested with larvae of *A. aegypti* and other mosquitos. Some measure of the degree of infestation was obtained by dipping a ladle into each drum and counting the number of *A. aegypti* larvae per ladle, compared with other species. Frequent counts showed that *A. aegypti* was always present, the average number per ladle over the period of the catch being nine compared with 19 of all the other seven species together.*

For a period of six months (November 1950 to May 1951), biting catches were made at the drums and in the usual catching places in bush on alternate days. The results of these captures were 112 by the drums and 185 in bush.

The higher captures in bush were not altogether expected but they serve to show that dispersion must be thorough, although there was no means of gauging its extent. This would also seem to be indicated by the flight from houses of immature females in large numbers and is in accordance with the findings of Shannon & Davis (1930).

The captures in bush were not made in one place but whilst the catching squad was moving slowly through the surrounding vegetation. The catchers sat for short periods (about 15 minutes) and waited for mosquitos to bite; they then moved on to another situation and waited again, repeating the process throughout the day; by the end of the day the drums had been encircled at least once. The squad never approached nearer than about 30 yd. or went further than about half a mile from the drums and there was no noticeable difference in the number of mosquitos caught, whether near or far from the drums. It could not be claimed that there were no other foci in the vicinity, although no breeding was detected and the captures were made in the drier part of the year, and it seems certain that the majority of mosquitos must have originated from the drums.

For a period of 28 days during the rains, when there were innumerable breeding places such as coconut shells, rot-holes in trees, fallen leaves and other water containers in the plantations, captures were made again, but in this case one day was spent in the same situation throughout the day while on the next the squad moved round as before; on the third day a different place was again selected in which the catchers remained throughout the day. By alternating these two methods daily, 172 females were taken by moving and 98 by stationary catches.

---

* *Aëdes* (*Stegomyia*) *metallicus* (Edw.); *Aëdes* (*Finlaya*) *longipalpis* (Grünb.); *Culex* (*C.*) *pipiens fatigans* Wied.; *C.* (*C.*) *decens* Theo.; *C.* (*Culiciomyia*) *nebulosus* Theo.; *Eretmapodites chrysogaster* Grah. and *E. quinquevittatus* Theo.

These results seem to imply that the flight of *A. aegypti* is a short one since, if it were long, there would be little difference in the captures by the two methods. It would appear that the stationary catches tend to exhaust the mosquitos in a circumscribed area around the place where the catch is in progress, and that more are collected in moving catches because the catchers proceed to a new place when an area becomes exhausted. As a corollary, dispersion is not, so to speak, instantaneous and it takes time to replenish the exhausted areas. Instances are known of *A. aegypti* travelling considerable distances (*cf.* Shannon, Burke & Davis, 1930, who record captures a thousand metres from the point of release), but these are believed to be exceptional.

Vertical Distribution.

Captures of biting mosquitos to demonstrate their vertical distribution have been undertaken by a number of workers and *A. aegypti* has often figured in these captures (Harris, 1942; Davis, 1944; Haddow, 1945; Haddow, Gillett & Highton, 1947; Haddow & Mahaffy, 1949; Garnham, Harper & Highton, 1946), but they were often incidental or too few for comparative purposes. A number (15) of twenty-four hourly captures was therefore made in a large mango tree in which two platforms were built, at 30 ft. and 50 ft., respectively, from the ground. Captures were made simultaneously on the platforms and on the ground under the tree. Among the many other species taken, there were four *A. aegypti* at 50 ft., 14 at 30 ft. and 37 on the ground (see Table IX), results which are consistent with the findings of the other workers elsewhere. Biting catches alone did not indicate whether the females were attracted to the bait from lower

TABLE IV.

Percentage of bamboo pots with *Aëdes aegypti* larvae in various situations.

Situation	Position	Percentage of pots with larvae
Coconut trees	In crown	14·6
	Half-way up	19·5
	At foot	31·0
In trees	Average height 25 ft.	16·6
Under trees	On ground	24·5
Under bush	On ground	26·7
In the open	On ground	15·5
In bananas	In axils	27·4
House	Inside	23·1
House	Outside	20·7

Five pots measured about 8 in. in depth and 2 to 3 in. cross-section were placed in each situation and examined at five-day intervals for a period of seven months. When larvae were found in them the pots were emptied, boiled in water and replaced. " Percentage of pots with larvae " is the number of records of pots that were found to contain larvae in each situation as a percentage of the total number of examinations of pots in that situation.

levels or whether they normally frequented the canopy of trees in plantations, and males, naturally, were not taken. The writer, by adapting Harris' (1942) use of bamboo pots for egg-laying had, however, earlier shown that *A. aegypti* will lay eggs 72 ft. above ground and that pots varying in height from 25 to 60 ft. above ground will frequently be used (Teesdale, unpublished report, Sect. med. Ent., Mombasa, Kenya, 1944). Table IV gives the percentage of pots, in a selection of environments, in which larvae were found.

Hence it may be taken that, on the Kenya coast, *A. aegypti* goes to considerable heights to feed and oviposit (*cf.* Garnham, Harper & Highton, 1946: no larvae found in pots placed in trees in the Kaimosi Forest, Kenya), but that its normal flight is near the ground is borne out by the higher captures of biting females under the tree as well as the ground-level percentages of pots used for egg-laying.

Window-trap Captures.

In order to procure more precise information on movements of adult *A. aegypti*, traps were fitted to windows in a number of houses in Jomvu village. The traps were made to fit window frames which were usually about two ft. square, and the traps themselves, box-like in shape, were constructed of wire gauze over a light wooden frame; the side which was fixed to the window was uncovered but had fitted to it on the inside a cone-shaped piece of mosquito netting with an apical opening one and a half in. in diameter; this aperture faced the centre of the opposite side of the cage, about four in. inside the gauze on that side. A circular opening on a third side was fitted with a sleeve for collecting trapped mosquitos. The traps could be fixed facing inwards or outwards to catch in-going or out-going mosquitos, respectively.

Fifteen houses were chosen with rooms having ceilings and only one window. Nine were fitted with exit traps, and six with entrance traps. A far greater number of out-going adults was invariably captured since, in a room with only one exit, the mosquitos probably showed a positive tropotactic response to the light or an escape reaction when disturbed. They were also more concentrated indoors, where breeding was almost always taking place.

The attraction of adults into the entrance traps on the other hand appeared to be slight. Stray mosquitos might be attracted to the shade under the thatched eaves of the houses and subsequently to the dark hole in the window opening or even by smell, but their capture must have been far more fortuitous than that of those leaving. In spite of this, considerable numbers were taken in entrance traps and a high proportion of them were males.

The curves for the two sexes, summed for 1950 and 1951, are shown in fig. 2; captures in corresponding months of each year were similar. The entry curves have been drawn to an enlarged scale because few mosquitos were captured entering houses, while those for seasonal distribution and meteorological data are added for comparison.

The out-going and in-going curves delineate the actual numbers captured in the traps each month, but those for seasonal distribution are based, in the case of house captures, on weekly searches in the houses kept as controls in the trial at Kwa Shekh described on p. 733, and represent the average number caught per house each month for the two years together. Those captured biting outside are based on a " biting index " obtained by dividing the total females captured per hour each day by the number of Africans employed on the catch.

The following facts may serve in some measure to explain the dissimilarity in these two curves, for house captures and biting outside, respectively.

That for biting captures probably does reflect to a certain extent the actual abundance of females during any given month, since the more there are present at the time of a catch the higher presumably will be the proportion that are ready to bite. This in turn will depend on a number of other factors, one of which—humidity—is likely to play an important part; a certain similarity is evident in the curves depicting relative humidity and biting captures. April–May and July–August are the months of highest relative humidity and these correspond with the two peaks in the biting curve (the much smaller size of the one in July–August may be due to the greatly reduced number of breeding places in June); while lower humidity generally corresponds with reduced biting.

In house captures, on the other hand, a higher proportion of the total *A. aegypti* population appears to be indoors during the months when biting-activity outside is at a minimum, or, as may be justifiably supposed, when the population out-of-doors is at a minimum. This tends to the probability that at certain times of the year (*i.e.*, from July to October) there is a general ingress of both sexes into houses. This supposition is supported by reference to the out-going and in-going curves, the former being at its minimum when captured mosquitos in houses and those entering them are at their maximum.

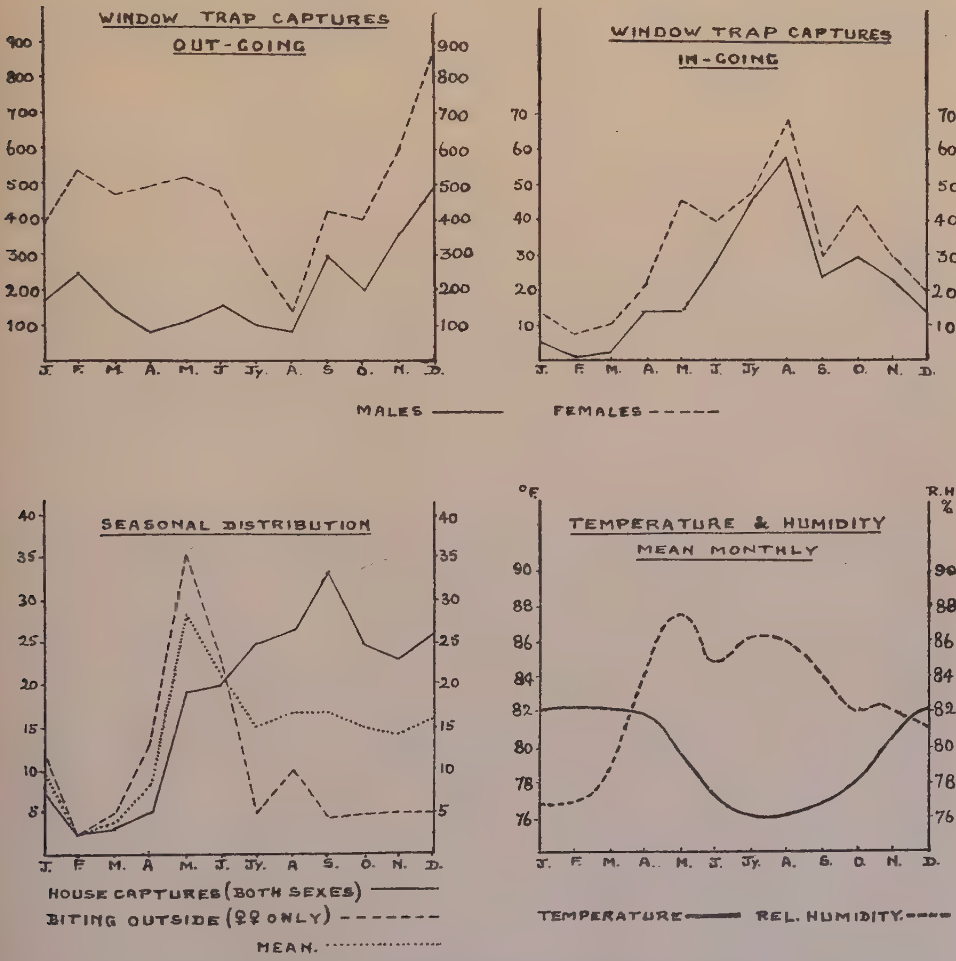


Fig. 2.—Captures of *Aëdes aegypti* at Jomvu and Kwa Shekh, summed for 1950 and 1951. Seasonal distribution and meteorological data for comparison.

The true curve for seasonal distribution therefore is likely to be near the mean of house and outside biting captures.

It is further evident that these two curves and those for in-going adults approximate closely during the hot dry months of January to March (when the total population is at its lowest), but that the contrary appears to be the case with regard to those leaving houses. No explanation is offered for this.

Readings taken during biting experiments showed that temperatures taken inside a house during the day were always a degree or so below those outside, but were higher during the night. Relative humidity, inside or outside, was always much the same during the day or night; it was, however, always lowest from 10 a.m. to 6 p.m. with a minimum between 1 p.m. and 2 p.m. These conditions differ from those recorded by Haddow (1942) at Kisumu where he showed that the range of relative humidity was much less in huts than in the screen outside. The Swahili houses on the coast differ in construction from those at Kisumu which probably afford better insulation.

The curves in fig. 2 are based on the sums of the monthly totals, for 1950 and 1951, of mosquitos collected daily from the traps at 7 a.m., 12 noon and 6 p.m. East African Standard Time. Mosquitos collected at 7 a.m. had therefore entered the traps during the hours of dusk, night and dawn. The results for the two years are summarised below.

Period	I		II		III				
E.A. Standard Time	6 p.m. to 7 a.m.		7 a.m. to 12 noon		12 noon to 6 p.m.		Total		Mosquitos
Sex	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	
Leaving	759	2161	292	651	936	1929	1987	4741	6728
Entering	41	125	44	45	14	46	99	216	315
Totals	800	2286	336	696	950	1975	2086	4957	7043
♂♂ & ♀♀	3086		1032		2925				

The captures indicate that *A. aegypti* left houses in about equal numbers between 6 p.m. and 7 a.m. and between 12 noon and 6 p.m. and that the proportions of males to females at the three collecting times was about 1:2·5. As regards those entering houses, more apparently did so during the hours of darkness than at other times and except for the 7 a.m. to 12 noon period the proportion of males to females was about 1:3. By grouping all males and females together for each of the three periods it was possible to obtain a general indication of flight-activity at these times. Thus it appeared to be lowest between 7 a.m. and 12 noon and highest between 12 noon and 7 a.m.

These findings were obviously too crude and in order to obtain a more detailed picture of this movement, collections were introduced, from August to December 1951, at hourly intervals daily (6 a.m. to 9 p.m.—fig. 3) and at weekly intervals during the night (9 p.m. to 6 a.m.); but in the latter only 14 males and 16 females were taken in the exit traps and four males and two females in the entrance traps.

The chief difference between these hourly captures and the previous ones was the negligible number of in-going males and females during the hours of darkness. Even allowing for only weekly catches between 9 p.m. and 6 a.m. it was soon apparent that activity declined sharply after 9 p.m. and remained at a low level until 6 a.m. It was therefore decided to compare data collected between these hours with those for the remaining 24-hour period from weekly captures in an entrance and exit trap both of which were in the same room. This was carried out over a period of 14 weeks and the results were as follows:—

	9 p.m. to 6 a.m.		6 a.m. to 9 p.m.		Total	
	♂♂	♀♀	♂♂	♀♀	9 p.m. to 6 a.m.	6 a.m. to 9 p.m.
Entering	4	2	51	19	6	70
Leaving	1	—	22	35	1	57

It was not possible to make collections at night from the entry traps in the other rooms as they were fitted to the inside of bedrooms which were occupied; but day and night captures were made in the exit traps on the same days as the two mentioned above. Results from these were:—

	9 p.m. to 6 a.m.		6 a.m. to 9 p.m.		Total	
	♂♂	♀♀	♂♂	♀♀	9 p.m. to 6 a.m.	6 a.m. to 9 p.m.
Leaving	11	15	52	120	26	172

It seems clear, therefore, that *A. aegypti* has little inclination either to enter or leave premises between 9 p.m. and 6 a.m. Humans are indoors between these hours and for this reason there may be some attraction into houses, but from the data on biting-activity (p. 727), it would not appear that they enter to feed.

Data collected from the exit traps from August to December 1951 (fig. 3, b) show that an increase in activity was evident at about 6 a.m. (daybreak), reaching its maximum between 7 a.m. and 8 a.m., after which there was a gradual decline until about 10 a.m.; from then onwards until two o'clock in the afternoon only a few mosquitos were captured, but after that a steady increase followed which reached its maximum between 5 p.m. and 7 p.m.

This bi-modal curve was less obvious in the entrance traps owing, perhaps, to the comparatively small numbers of adults captured (fig. 3, a). The marked ingress of males between 10 a.m. and 11 a.m. can, however, hardly be passed over as being without significance since this is the time when out-going mosquitos of both sexes as well as in-going females were least in evidence.

If the lull in activity at about this time be construed as part of a general activity rhythm in these three groups (out-going males and out- and in-going females) there seems no reason why the same rhythm should not be evident as regards the in-going males; but since this is not so it may be presumed that at about this time some external influence acts upon males in outside harbourages in such a way that the normal rhythm is broken. It is difficult, however, to imagine any such influence that would not be equally applicable to females. The only explanation seems to be that humidity, temperature or light intensity outside (or a combination of them) reach a threshold at about 9 a.m., above or below which males are stimulated to seek shelter. This threshold may be reached sooner in the case of females (8–9 a.m.) and in this event the earlier movement of this sex (as shown in fig. 3, a) would be accounted for.

Further points of note in connection with captures in window traps are:—

1. Although both sexes were captured in the exit traps from the time they were first put into operation, no mosquitos were taken in any of the entrance

traps for the first month (over eight months in the case of one trap). Furthermore, when the mosquitos had started to enter they generally did so for a few days only and then stopped. Thus No. 1 trap was put into position on 21.i.1950 and no mosquitos were captured in it until 22.iv.1950 when the total taken for the week commencing on that date was three males and six females; the following week one more male and 11 females were taken and then nothing more for a further four months.

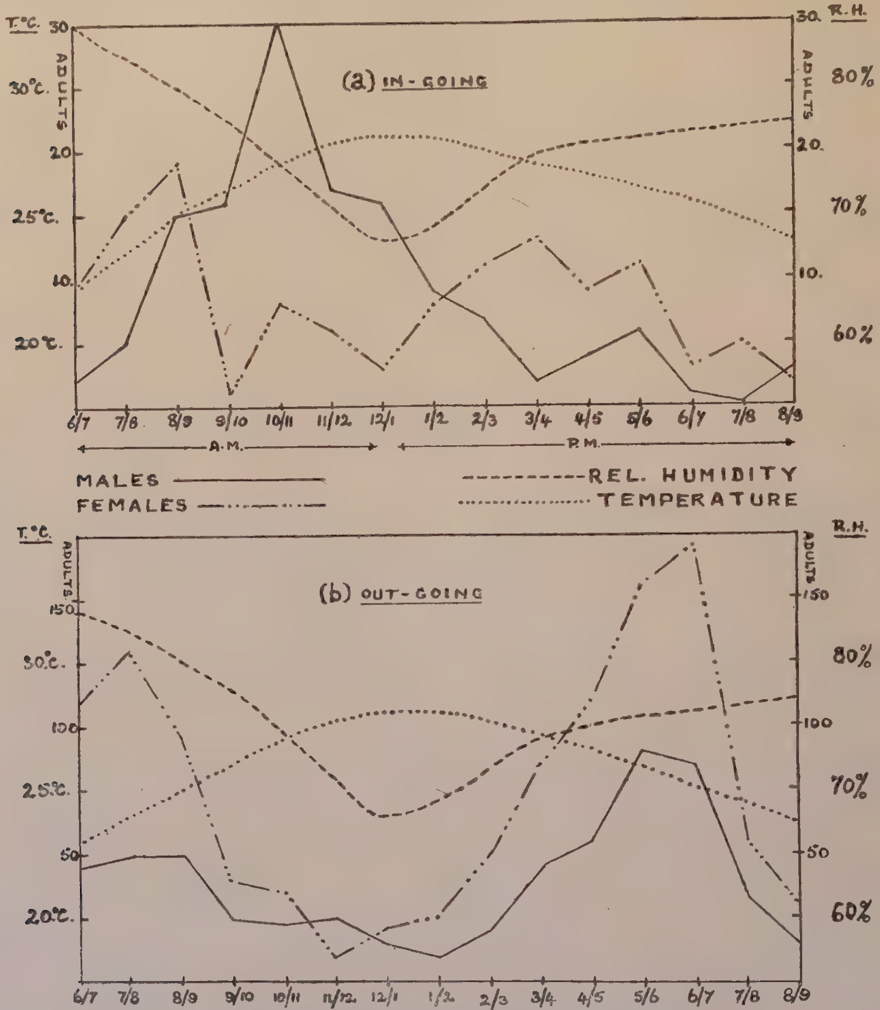


Fig. 3.—Captures of *Aëdes aegypti* in window traps at Jomvu to show times of entry and exit, respectively, Aug.–Dec. 1951. (6 a.m. to 9 p.m. only.)

It was thought that the presence or absence of breeding in the vicinity might account for this, but in only one instance could it be said to apply. This was in the case of trap No. 6 that was sited about 15 yd. from a large cement tank of water which was situated outside a mosque and produced large numbers of adults for long periods. Captures in this trap were always higher than in any of the others. Two more empty traps were therefore fixed to the windows of occupied rooms even nearer the tank (at six and ten yd. distance, respectively), but no mosquitos were found in either of them, even though they were in position for nearly three months. No explanation was found to account for these conditions. Orientation of the traps in relation to the points of the compass and the prevailing wind was tested by noting the numbers of adults captured in all the other traps and the direction in which the openings of these faced, but no significant difference was found in the number of mosquitos taken.

2. Both sexes continued to enter rooms for some weeks after these were no longer occupied, a fact which strengthens the suggestion that *A. aegypti* does not enter houses only to feed.

Having established the fact that *A. aegypti* habitually enters and leaves native dwellings with a preference for doing so at certain times and seasons, the natural corollary was to attempt to discover the reasons for this movement. They may have been connected individually or in combination with oviposition, mating, feeding or sheltering.

Ovulation and Digestion.

Christophers' (1936) method of measuring ovarian development was adopted and, in a simplified form, that of Hocking & MacInnes (1948) for blood digestion. These authors describe the external characters of *Anopheles gambiae* Giles and *A. funestus* Giles which correspond with Christophers' five stages.

From August 1950 to the end of July 1951 ovary examinations were made of those females which had been collected from window traps at 7 a.m., 12 noon and 6 p.m. Results are shown in fig. 4.

In spite of there being far fewer in-going females, on a percentage basis it was clear that:—

(a) The highest proportion leaving were Stage V.
(b) A fair percentage of Stage I left houses between all three collecting times.
(c) The highest captures of Stage I in the entrance traps were taken at 7 a.m., whereas Stage V captures were highest at 6 p.m.
(d) Intermediate stages were proportionately few.

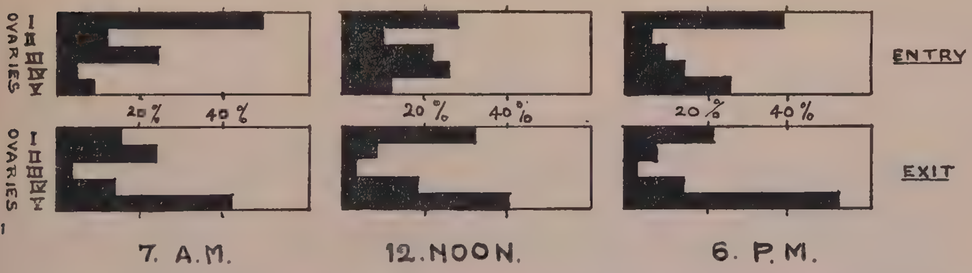


Fig. 4.—Window-trap captures of *Aëdes aegypti* at Jomvu. Stages of ovarian development at different times of exit and entrance.

Time	Total	
	Out	In
7 a.m.	1084	44
12 noon	495	38
6 p.m.	1528	59
	3107	141

Examinations from hourly captures carried on for 17 weeks from 7 a.m. to 9 p.m. gave similar results.

Very few Stage V went in at any time, but in the exit traps females at this stage were again most in evidence, with the highest captures between 7 a.m. and 8 a.m. and from 4 p.m. to 7 p.m. At almost every hour the percentage in Stage V was higher than in any other stage and Stages I and IV were next most in evidence. (See fig. 5.)

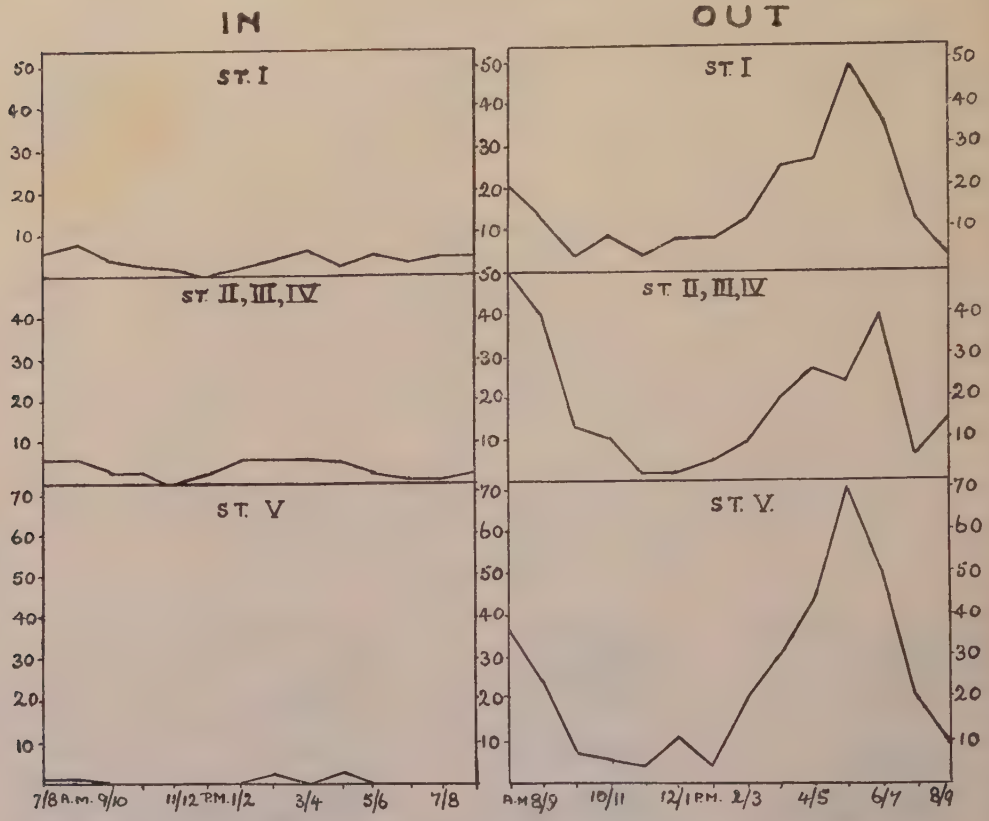


Fig. 5.—Exit and entry curves of *Aëdes aegypti* in different stages of ovarian development from window-trap captures at Jomvu, Aug.–Dec. 1951.

Dissections of night captures from exit traps (9 p.m. to 7 a.m.) actually showed the highest proportion in Stage II, but the numbers were considered too few to be significant.

A note was also made of the condition of the abdominal contents of all females dissected. The condition was divided into four categories as follows:—(a) Unfed. (b) Blood fresh. (c) Blood partially or well digested. (d) Digestion complete. Correlation of these conditions with ovarian development is given in Table V.

The picture in Table V is typical, the ovarian development proceeding alongside digestion with no unfed females being taken after the ovaries were past Stage I. This confirms the second part of the finding of MacGregor (1931) that the requirements of ovulation are sperm in the spermatheca and blood in the stomach.

TABLE V.

Digestion and ovarian development in *Aëdes aegypti* captured in exit window traps at Jomvu.

Ovaries (Stage)	Time captured	Unfed	Blood fresh	Blood partly digested	Digestion complete
I	7 a.m.	172	171	—	—
	12 noon	146	27	—	—
	6 p.m.	337	81	—	—
II	7 a.m.	—	106	—	—
	12 noon	—	21	—	—
	6 p.m.	—	44	6	—
III	7 a.m.	—	10	25	—
	12 noon	—	7	11	—
	6 p.m.	—	5	45	—
IV	7 a.m.	—	—	76	92
	12 noon	—	2	40	41
	6 p.m.	—	—	82	127
V	7 a.m.	—	—	350	105
	12 noon	—	—	178	58
	6 p.m.	—	—	651	213

Subsequently both out-going and in-going females were dissected and the following results obtained:—

TABLE VI.

Ovarian development and digestion in female *Aëdes aegypti* captured in entrance and exit window traps, Jomvu, 1951.

	Exit traps					Entrance traps				
Stages:	I	II	III	IV	V	I	II	III	IV	V
Unfed	235	—	—	—	—	50	—	—	2	—
Blood fresh	76	36	4	3	—	4	3	4	1	—
Blood partly digested	9	—	10	87	321	—	—	6	10	4
Digestion complete ..	—	—	—	71	10	—	—	6	18	—
Totals	320	36	14	161	331	54	3	16	31	4

The number of Stage V females entering houses is again in marked contrast to those leaving; but there is nothing to indicate any physiological difference in the two groups. The two Stage IV mosquitos caught in the entrance traps, which were apparently unfed, cannot be accounted for.

The tendency for gravid females to leave houses and those with immature ovaries to enter them suggested that the gravid ones might be going outside to oviposit while young ones entered in order to shelter, to feed or to mate.

It is known that on the Kenya coast *Aëdes aegypti* lays both outside and in houses (*cf.* Kerr, 1933, who contends that in West Africa the mosquito is not found out-of-doors) and there were certainly facilities for egg-laying indoors in all the houses to which traps were fitted. It does not, therefore, seem reasonable to suppose that the egress of gravid females was entirely connected with oviposition.

As already mentioned, females taken in intermediate stages of ovulation were comparatively few in number when compared with those in Stage I or V, but this was not unexpected as they would presumably be resting while digesting their blood-meal and maturing their eggs.

As regards young females, it was considered that opportunities for feeding were almost as good outside as inside, and tests with human bait showed that females fed just as readily out-of-doors as indoors (fig. 7). On the other hand, the influx may have been due simply to a search for shelter; but the possibility of it also being connected with mating could not be overlooked. It was therefore decided, as a next step, to examine the spermathecae of all females taken in both kinds of traps and also of those caught biting out-of-doors (see Table VII).

When the spermathecae were dissected the stomach was also examined, but only three females with Stage I ovaries, out of a total of 67 captured out-of-doors using human bait were found to have had a blood-meal; it seems obvious that the three engorged females had succeeded in feeding on the catchers before they were captured.

Owing to the small numbers that entered houses and to the lack of opportunity to extend these catches until sufficient numbers were taken, practically all those examined came from the exit traps; but a fair proportion were also captured out-of-doors at Kwa Shekh and on Mombasa Island where human bait was used to attract the females.

TABLE VII.

Fertilisation and its relation to feeding and ovulation in *Aëdes aegypti.*

Stages :	I		II		III		IV		V	
	Exit traps	Biting outside	Exit traps	Biting outside	Exit traps	Biting outside	Exit traps	Biting outside	Exit traps	Biting outside
Number examined	199	67	8	1	12	0	98	1	89	1
Number fed	0	3	3	1	12	0	98	1	89	1
Number fertilised	0	0	3	1	12	0	98	1	84	1
Number unfertilised	199	67	5*	0	0	0	0	0	5*	0

From entrance traps:—
Stage I: examined, 3; fed, 0; unfertilised, 3.
Stage V: examined, 1; fed, 1; fertilised, 1.

* Five Stage II and five Stage V females were apparently unfertilised; but it is known that in many mosquitos a blood-meal alone is sufficient to stimulate ovulation which may proceed until the eggs are ready to be laid. This may be so with *A. aegypti*, but as far as is known the phenomenon has not been recorded in this species.

Since so few immature, unfertilised females were captured entering houses it appears probable that their entry had no connection with mating, and since none of the 199 leaving had fed, it might follow that only *A. aegypti* which emerge indoors bite indoors, and that those which originated from outside had entered with the intention of sheltering only. The same may be said of the 235 unfed ones shown in Table VI, and that the remaining 76 which contained fresh blood were those which had hatched out inside, taken advantage of the opportunity to feed and were leaving in order to pair. This supposition does not of course take account of the fact that those which had entered from outside might also have had an equal opportunity to feed, but it does support the suggestion that they do not enter houses expressly for that purpose.

The Biting-cycle.

It was felt that information on the biting-cycle of *A. aegypti* might further elucidate what had already been determined regarding flight and fertilisation. Catches during the day from 7 a.m. to 7 p.m. had been recorded on Mombasa Island and at Kwa Shekh at hourly intervals from May 1949 to January 1952. African volunteers were used as bait and the captures were made outside in sheltered situations. The volunteers varied in number from three to nine and

TABLE VIII.

Daytime captures of biting *Aëdes aegypti* in plantations and bush, Mombasa Island and Kwa Shekh, May 1949 to January 1952.

Time	Number of *aegypti*		Period of catch in hours		Index*		Composite index
	Mombasa Island	Kwa Shekh	Mombasa Island	Kwa Shekh	Mombasa Island	Kwa Shekh	
6/7 ..	86	3	122	105	7·0	0·3	3·7
7/8 ..	250	131	245	224	10·0	6·0	8·1
8/9 ..	232	91	245	225	9·5	4·0	6·9
9/10 ..	244	83	242	226	10·1	3·7	7·0
10/11 ..	446	151	239	215	18·6	7·0	13·1
11/12 ..	314	179	236	215	13·3	8·3	10·9
12/1 ..	360	129	234	216	15·4	6·0	10·9
1/2 ..	171	117	234	218	7·3	5·5	6·4
2/3 ..	180	120	232	221	7·7	5·4	6·6
3/4 ..	214	129	237	221	9·0	5·8	7·5
4/5 ..	596	215	240	209	25·0	10·3	18·0
5/6 ..	603	184	241	212	25·0	8·7	17·4
6/7 ..	604	174	118	105	51·2	16·6	34·9
Totals ..	4311	1706	2865	2612			

$$* \frac{\text{Total mosquitos captured}}{\text{Number of hours of search}} \times 10.$$

were stripped to the waist. They first worked together as a gang, sitting in the vegetation and waiting for mosquitos to bite; later, they were divided into three small groups of three each, which worked independently although they made their captures in the same area. Each member was issued with wide-mouthed test tubes which he used to capture mosquitos biting his own person or the backs of his comrades. At Mombasa and Kwa Shekh the times both of maximum and minimum biting-activity coincided (Table VIII). The biting-cycle is indicated graphically in fig. 6.

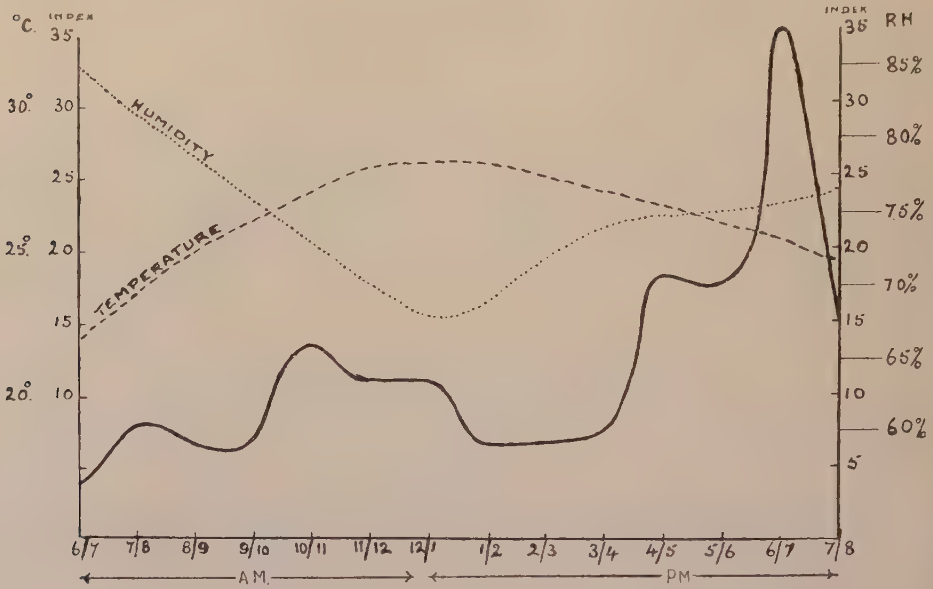


Fig. 6.—Diurnal captures at hourly intervals of *Aëdes aegypti* biting outside at Mombasa and Kwa Shekh, May 1949 to January 1952.

The curve indicates that, although *A. aegypti* will bite at all hours of the day, there is a characteristic type of behaviour with a small peak between 10 a.m. and 1 p.m. and a greater one from 4 p.m. to 7 p.m. The curve is continued until 8 p.m. to show that from 7 p.m. onwards biting is much reduced. (The curve falls steeply to 9 p.m. and then remains near zero throughout the night.)

The increase in biting-activity between 7 a.m. and 8 a.m. is more marked than would appear from the graph; there is often a sharp rise in activity at about this time followed by a marked falling off until 10 a.m. This peak and that of the late afternoon correspond with those of fig. 3, a (p. 722), which denote the exit times from houses of both males and females; but the mid-morning peak for biting corresponds with a distinct decrease of both sexes in the flight curve.

These data certainly strengthen the supposition that *A. aegypti* does not enter houses to feed, while the times of biting (fig. 6) and flight from houses of both Stage I and V females (fig. 5), though not identical, are near enough to suggest strongly that hungry females go outside to feed in the late part of the day and gravid ones, as already indicated, leave to oviposit.

Factors Influencing the Urge to Bite.

Twenty-four hour catches were also undertaken inside a house, outside houses in the village and on platforms in a mango tree in the plantations. Fifteen such catches were made in each place at different times of the year and the results are shown in Table IX. Captures were disappointingly few but they were sufficient to indicate the general trend of biting-activity and demonstrate that *A. aegypti* bites throughout the 24-hour period, although it is much less inclined to do so during the hours of darkness.

TABLE IX.

Result of fifteen 24-hour captures of biting *Aëdes aegypti* in different environments at Kwa Shekh, 1950 and 1951.

	Platform						In a House				In the Village			
Time	Ground	30 ft.	50 ft.	Temp.		R.H. %	Mosq.	Temp.		R.H. %	Mosq.	Temp.		R.H. %
				W.	D.			W.	D.			W.	D.	
a.m.														
6– 7	3	2	—	21·5	22·9	88	4	22·5	24·8	83	9	22·0	24·3	82
7– 8	1	—	—				5				11			
8– 9	2	1	—				4				10			
9–10	1	1	—	23·2	26·1	78	15	23·6	26·8	78	18	23·2	26·2	78
10–11	1	1					16				15			
11–12	—	—	—				15				13			
p.m.														
12– 1	—	—	—	23·6	27·9	68	8	24·1	28·7	69	6	23·3	28·5	65
1– 2	1	2					7				7			
2– 3	2	—	3				8				8			
3– 4	2	1	—	23·5	28·0	68	5	24·0	28·4	68	6	24·2	28·7	69
4– 5	3	5	—				3				5			
5– 6	10	—	—				5				25			
6– 7	7	—	—	23·3	26·1	79	11	23·3	26·4	78	7	23·6	26·3	80
7– 8	2	—	—				1				7			
8– 9	2	—	—				—				5			
9–10	—	—	—	22·7	25·0	82	2	23·6	26·3	80	2	23·2	26·0	79
10–11	—	—	—				1				3			
11–12	—	—	1				—				6			
a.m.														
12– 1	—	—	—	22·7	23·9	89	1	23·4	26·0	81	3	22·8	25·3	81
1– 2	—	—	—				2				2			
2– 3	—	—	—				—				1			
3– 4	—	—	—	22·7	24·3	88	1	22·8	25·0	83	1	23·0	25·2	77
4– 5	—	1	—				1				3			
5– 6	—	—	—	22·5	23·5	—	3	—	—	—	6	—	—	—
	37	14	4				118				179			

The morning and late-afternoon periods of activity are discernible, but if the numbers captured are placed in three-hourly groups a rather different picture of biting-activity is produced. If the first period starts at dawn (6 a.m.) the morning peak (9 a.m.–12 noon) is evident both inside and outside the house, but not in and under the mango tree (where only a very few females were caught biting). The late-afternoon peak, however, is present in both outside situations, but not in the house (fig. 7).

The reason for this departure from the normal rhythm can only be ascribed to the fact that the catch took place in the very confined space of a small room. The effects upon biting in such situations are discussed under " The Activity Rhythm " (p. 737).

Wet- and dry-bulb readings were taken with a whirling hygrometer at three-hourly intervals. This could not be done simultaneously in the three situations, but a general comparison of all readings at any given hour showed that the differences in relative humidity were very slight indeed. Temperatures were very uniform in all situations at the same hours and the average daily range was only 4·7°C. in houses and 5·9°C. outside, with maximum ranges of 6·0°C. and 9·0°C., respectively.

The day and night captures may be summarised as follows:—

Catching period	In a house	In the village	Mango tree
Day (6 a.m.–7 p.m.)	102	131	16
Night (7 p.m.–6 a.m.)	16	48	2

The night to day proportion of females biting inside a house is not as high as that of those biting outside in the village. Mattingly, however, in eight 24-hour catches in houses at Ogbomosho, Nigeria, obtained the following approximate figures (personal communication):—

Period (Nigerian Standard Time)	*A. aegypti* captured biting
1500 hr.–2100 hr.	8
2100 ,, –0900 ,,	41
0900 ,, –1500 ,,	8

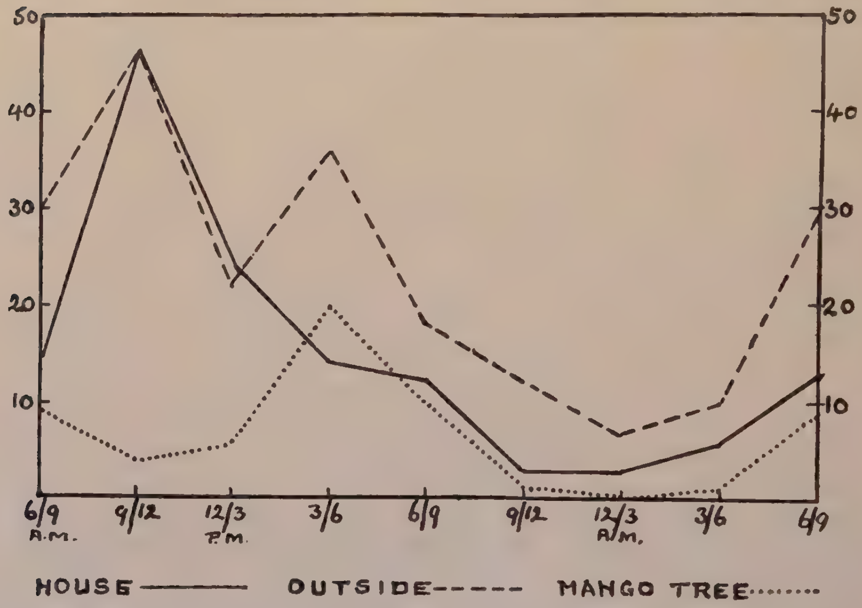


Fig. 7.—Fifteen 24-hour catches made (1) in a house, (2) in the village and (3) at a mango tree to demonstrate biting-activity of *Aëdes aegypti*, Kwa Shekh and Jomvu, 1950 and 1951. Catches grouped into three-hour periods.

If *A. aegypti* behaves at Ogbomosho as it does on the Kenya coast, the period 2100 hr. to 0900 hr. would include the early morning peak of activity, but even so it seems probable that, in houses, many more females were taken biting during the hours of darkness than during those of daylight, which is the opposite to what has been revealed in the present investigations.

It is thought that the house captures at night here described may have been influenced by the use of electric hand torches which were used almost incessantly throughout the night, since Seaton & Lumsden (1941) found that at temperatures closely resembling those in the present catches, direct illumination of 0·5 metre-candles at the area to be bitten reduced the number of *A. aegypti* feeding by nearly half.

Night and day captures of biting *A. aegypti* may not therefore be strictly comparable when hand torches are employed at night and in this case their use may have reduced the numbers of females which would otherwise have fed. As similar methods were presumably used at Ogbomosho, comparison with findings there should be permissible.

During the whole of 1950 the effect of direct sunlight on feeding was checked by dividing the catchers into two squads which worked close together, but one was always in full sunlight while the other kept in the shade of trees or bushes, and they were changed about every day. The results (Table X) show that higher catches were always made in the shade (407 against 82). It was noticeable that females which were caught in the sun generally, but by no means always, chose a shaded part of the body when they bit.

Host Preferences.

Monkeys and galagos captured in coastal forests have shown immunity to yellow fever (Haddow, 1952) and may well prove to be the reservoir of the virus of the sylvatic form of the disease. The biting catches mentioned above have indicated the predilection of *A. aegypti* for human blood; but the vector (or vectors) of the disease in Kenya are as yet hypothetical and it was felt that precipitin tests of the stomach contents of females which had fed might show whether there were hosts other than man.

Smears were therefore made from the blood of females captured in the plantations and a representative number was sent to Dr. B. Weitz of the Lister Institute of Preventive Medicine to whom the author owes his thanks for undertaking the tests.

One hundred and five specimens were first submitted but 54 of them were found unsuitable for testing. Although the remaining 51 were tested for man, monkey, ox, goat, cat, dog, rat and fowl, only eight (or 16%) proved positive to man and these and all the others were negative against the remaining antisera. The 54 unsuitable specimens were also tested with all the antisera, but, as was expected, proved to be negative.

These results clearly indicated some other important host, and a further 244 smears were therefore submitted. Of these only 75 were suitable, and this time 51 (or 68%) were positive to man, while they and the remaining 24 were all negative to the other seven antisera.

The results of the second test show little resemblance to those of the first, yet with the exception of 13 mosquitos which were taken in hand nets while flying,* all the rest, in both tests, were captured under identical conditions and in the same environment—in the plantations during "biting" catches. A very high proportion of them was caught before they had had time to feed, which probably accounts for the large number classed as unsuitable; but all of the 126 tested had had a meal, of which, as the results show, 47 per cent. had been on man. The remaining 53 per cent. had therefore fed on some other host not included in the seven antisera used.

Other mammals which are found in the plantations include hedgehogs, elephant-shrews, galagos, hares, mongooses and bats, only the last of which can be said to be abundant. As regards reptiles, lizards of many kinds, including the large monitors, are common. Except in the rainy season, when the swamps are full of water, frogs are not generally seen, but there are many kinds of birds.

Antisera were not available from any of these animals and they could not therefore be tested, but it seems unlikely that the mammals, with the possible exception of bats, are important hosts. As regards birds, all the tests were negative for domestic fowl, a fact that does not necessarily imply that the

---

* Four were positive for human blood; all were negative for the other antisera.

TABLE X.

Captures of biting *Aëdes aegypti* in sun and shade in plantations at Kwa Shekh, 1950.

Time	Jan.		Feb.		Mar.		Apr.		May		June		July		Aug.		Sept.		Oct.		Nov.		Dec.		Total	
	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.	S.	Sh.
7– 8 ..	—	—	—	1	1	—	3	6	—	5	1	—	—	—	—	4	—	3	—	3	—	1	—	2	5	25
8– 9 ..	—	2	—	—	—	—	—	2	—	2	—	—	—	2	2	9	—	1	3	2	1	1	—	—	6	21
9–10 ..	—	1	—	1	—	—	—	2	—	4	—	3	1	—	—	1	1	2	—	—	—	2	—	2	2	18
10–11 ..	—	—	—	—	—	3	—	3	7	17	—	—	—	5	2	4	—	4	—	3	—	—	1	1	10	40
11–12 ..	—	1	—	—	—	1	—	11	4	13	—	3	1	2	—	3	1	4	—	5	—	1	—	—	6	44
12– 1 ..	—	1	—	—	—	3	—	1	1	20	—	1	2	3	—	1	—	4	—	1	—	—	—	—	3	35
1– 2 ..	—	5	—	—	1	—	2	4	3	10	—	2	1	1	—	1	—	—	—	1	—	1	—	2	7	27
2– 3 ..	—	3	—	—	1	2	—	3	—	14	—	3	—	3	—	2	—	—	1	2	—	—	3	1	5	33
3– 4 ..	—	4	—	—	—	—	—	2	1	13	—	1	—	1	2	3	3	—	—	—	—	3	—	—	4	29
4– 5 ..	—	3	—	—	—	3	—	9	—	17	—	1	1	5	—	5	3	7	2	4	3	2	—	—	9	56
5– 6 ..	1	2	—	1	1	1	2	3	—	9	2	3	3	5	3	6	—	2	—	2	1	1	—	—	12	36
6– 7 ..	2	2	—	—	2	1	3	4	—	17	—	3	—	1	3	6	—	4	1	5	2	—	—	—	13	43
	3	24	—	3	6	14	10	50	16	141	3	20	9	28	12	45	8	31	7	28	7	12	4	8	82	407

S = Sun, Sh = Shade.

mosquito does not feed on other birds, but if the host were avian, some indication of this might have been expected from the fowl antisera.

It is probable that although *A. aegypti* has certain host preferences, hungry females will feed on a number of other animals when opportunity offers. Reptiles, which were not tested at all, might well be included among them. Woke (1937*a*, *b*, *c*) has shown that viable eggs are laid by this mosquito after a feed on turtle and frog and that more eggs are produced after feeding on turtle, frog, canary and rabbit than on man or monkey. On the other hand, Toumanoff (1949) found that *A. aegypti*, which fed on lizards and geckos, did not produce as many eggs nor live as long as those which had fed on human blood. However, lizards are ubiquitous and easily accessible to mosquitos and, except that they themselves feed on insects and may almost certainly be excluded as a reservoir of yellow-fever virus, there seems no reason why in nature they should not serve as hosts (possibly geckos during the day and lizards at night—times when they are inactive?).

Unfortunately, examinations could not be made of individual cells from the precipitin smears in those cases where the blood was fresh, otherwise the presence or absence of nuclei might have indicated whether the hosts had been other than mammals.

On the other hand, monkeys and galagos are seen from time to time in the plantations, although they are not nearly so common as in the coastal forests. There, too, *A. aegypti* is present at considerable distances from human habitations; but platform catches made in the Gede forest by Bailey (1947) suggested that *Aëdes adersi* (Edw.) was the common arboreal mosquito.

The Effect of Domestic Larval Control on Adult Infestation in Houses.

It had been found in South America (Soper & others, 1943) that breeding of *A. aegypti* could be controlled, and the mosquito eradicated in towns, by intensive "species sanitation" measures which included the destruction of larval foci at regular inspections of premises. Experience during the past ten years in coastal towns of Kenya, however, has shown that breeding may be very nearly but not quite prevented by the application of the methods used so successfully in South America but that any extension of the interval between inspections beyond two weeks soon resulted in a return of both larvae and adults. Even when breeding had been reduced to negligible proportions over a prolonged period a few adults were always present (Teesdale, unpublished report, Med. Dep. Kenya, 1944).

It was decided, therefore, to investigate more closely the occurrence and behaviour of these adults, and larval control on the lines practised in South America was introduced at Kwa Shekh in the 36 houses in the village and in 22 other houses scattered through the surrounding plantations; a further 36 houses were kept as controls.

At each inspection of a house, adults were searched for with the help of a torch and "catching tube", the latter consisting of a six-inch glass cylinder of one-inch diameter with a small recessed opening at one end and a half-inch rubber tubing attachment at the other.

The results (fig. 8) show that larvae and adults were rapidly reduced by weekly inspections, the curves for both being very similar, but that it was impossible to maintain complete control for more than a few weeks at a time. These conditions suggest that the eradication of *A. aegypti* on the Kenya coast cannot be achieved by domestic larval control at weekly intervals and that no purpose would be served by more frequent inspections since tests have indicated (p. 715) that the life-cycle of the mosquito is completed in not less than eight days.

A marked diminution in the numbers of *A. aegypti* taken in the houses kept as controls occurred during the hot, dry period from January to March, despite the fact that just as many potential breeding places were to be found indoors as at other times of the year. This diminution in numbers is thought to be due in part to a reduction in the number of outside breeding places and in part to the less favourable conditions of temperature and humidity prevailing during the period in question, these factors combining to reduce the number of adults entering houses with a concomitant reduction in indoor breeding. The curves shown in fig. 1 (p. 713) represent temperature and humidity at those times of year associated respectively with the greatest and least abundance of *A. aegypti* in houses.

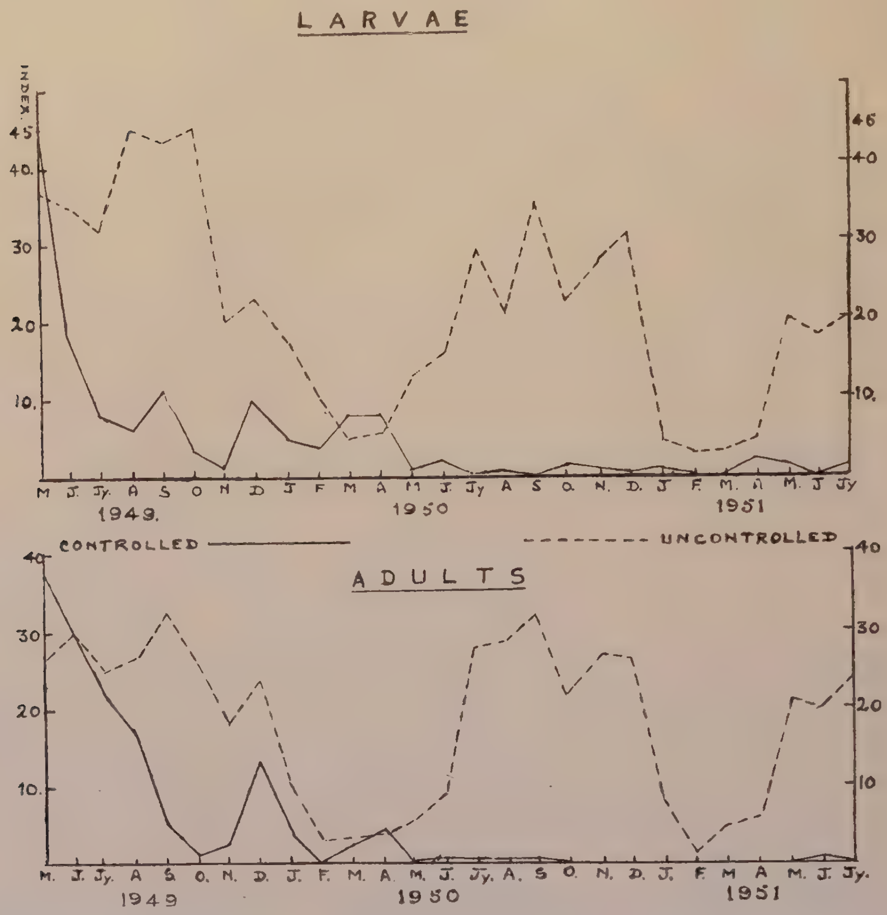


Fig. 8.—Reduction of larvae and adults of *Aëdes aegypti* by domestic larval control at weekly intervals. Catches in houses, Kwa Shekh, May 1949 to July 1951.

A few adults were sometimes found in houses in the cool months even after breeding inside had been completely prevented for some weeks, so these adults had presumably entered from outside and may have been responsible for the occasional recurrence of breeding. If this is so it serves to emphasise that eradication of *A. aegypti* cannot be secured by house control alone but will necessitate outside control as well.

Discussion.

The work described in this paper raises a number of points, which are discussed below.

Fertilisation, ovulation and feeding.—It would seem from the exit-trap figures that *aegypti* does not pair indoors, although this is a complete departure from well-known habits in the laboratory where the species is known to mate readily in a confined space. Although the author has often been present in rooms heavily infested with both sexes when emergence is taking place, he has never witnessed pairing indoors, nor have any records of its occurrence been noted except for a doubtful one by Goeldi (1905). According to Howard, Dyar & Knab (1912), copulation takes places at the brightest part of the day and this, if an invariable occurrence, might account for the absence of swarms in dark native dwellings. *A. aegypti*, as is well known, breeds in complete darkness in the laboratory.

Although Seaton & Lumsden (1941) found no difference in the desire for a blood-meal between virgin and fertilised mosquitos aged from 72 to 96 hours, the fact that every one of 269 Stage I females was unfertilised, whether captured leaving or entering houses or whether taken outside, confirms the finding of Cardamatis (1929) that mating does not take place until after the female has fed. The marked preponderance of Stage I females captured biting humans is to be expected, as hungry specimens are more likely to be attracted. It also agrees with the conclusions drawn from Table VI that those in later stages have fed at least once.

Twenty-four hour catches indicated that *A. aegypti* bites throughout the 24 hours, with a general trend towards two peaks of activity, in the morning and late afternoon, respectively, and a greatly reduced inclination to bite during the hours of darkness.

Thus it seems that the behaviour of *A. aegypti* in nature is in marked contrast to that which is manifest in the laboratory in the following three ways:—

1. Pairing only takes places after the first feed, while in the laboratory it appears to be quite independent of a blood-meal.
2. Pairing does not occur indoors, whereas it takes place in an indoor laboratory even in a very confined space.
3. Females practically cease to bite at night, while in the laboratory they will bite at any time.

If these findings are correct—and with the possible exception of the second there is nothing in the evidence which seems to suggest that they are otherwise—then it appears that under natural conditions some other influence is at work which is not present in the laboratory. In no case were there any indications to show what the nature of this influence might be. All that can be said is that conditions in a laboratory, however closely they may approximate those in nature are nevertheless artificial to a greater or less degree. However, the refutation of long-established facts obtained in laboratories cannot be accepted *in toto* without further careful tests under natural conditions, the chief aim of which would seem to be along lines which would indicate the nature of the influences which can cause such wide differences between mosquito behaviour in the two environments.

Flight and Dispersion.—In and around Mombasa the population of *A. aegypti* outside never seemed to be as dense as that of some other species (*Aëdes pembaensis* (Theo.), for instance) and for this reason it was felt that continuous catches, even if carried on for a considerable time, would not produce sufficient numbers of mosquitos on which to base conclusions. By using the drums described on p. 716 as a means of increasing the population of *A. aegypti*, and by catching alongside them, the captures, as has been shown, were not, however, increased and more mosquitos were taken by moving round at some distance from the drums. This was not altogether unexpected as, earlier on Mombasa Island, catches had not increased near a hidden soakage pit which was producing many adults, although they had done so in the neighbourhood. Heisch, on the other hand, one late afternoon took a large number of *A. aegypti* beside a waste-water sump behind his house in Nairobi where they were breeding (personal communication).

It is possible that in Nairobi the captures were made at a time when a large batch of adults was hatching and that the mosquitos had not had opportunity to disperse, but that on Mombasa Island and near the drums at Kwa Shekh eggs had been laid over a long period and hatching was thus continuous and not so concentrated as at Nairobi; besides this, the fact that captures were only made by day in Kwa Shekh afforded opportunities for adults to scatter between catches.

For these very reasons captures near the drums served, as was intended, to measure power of dispersion. This faculty of mosquitos is, however, extremely difficult to assess; release of marked specimens at a given point and subsequent collecting in concentric circles of ever-widening depth, under changing conditions of surface cover and weather, seems the only way to measure the phenomenon, but even then may give only a measure of the length of flight rather than the power of dispersion. It has been shown that *A. aegypti* can cross from Mombasa Island to the mainland, a distance of some 600 to 800 yd. (Wiseman & others, 1939), but this was considered exceptional. The simple method described here indicates that dispersion may be thorough without the flight range being a long one.

Vertical distribution and hosts.—Although it has been shown, by the presence of eggs in containers placed in the crowns of palm trees, and, to a less extent, by records of biting, that movement at higher levels does take place, flight is largely restricted to near ground level. It is therefore improbable that *A. aegypti* is involved in the transmission of sylvatic yellow fever where monkeys and galagos are concerned and on the coast these animals may not be the sole reservoir of the virus. Precipitin tests show that there is some host of *A. aegypti* other than man or the common domestic animals and since the mosquito's normal flight is a low one it suggests that this host is an animal which lives on or near the ground. Thus of the remaining mammals which are to be found on the Kenya coast (except those in forests and numerous small ground or burrow-frequenting species of typical bush) bats are the only other common mammal. and their habits would seem to preclude much chance of any association with *A. aegypti*.

Window traps.—The factors which influence flight of mosquitos into and out of houses, such as weather conditions, mating and feeding, have all been deduced from captures made in window traps, a method which seems the only practical way of assessing the numbers of the sexes entering and leaving and the times at which they do so; the main drawback to their use is the uncertainty as to whether the data collected from the exit and entrance traps are strictly comparable.

Although in this case their construction was identical, it seems certain that mosquitos were more readily attracted to the exit traps than into the entrance ones. Even if allowance is made for this possibility, it is almost certain that fewer mosquitos enter houses than leave them, because not only do they breed inside and in consequence are concentrated there, but it seems clear that those which have entered do not remain inside; thus, although the exact ratio between those going in and out may not be correct, the times of entry and exit and the proportion of males to females are.

One of the most difficult things to understand is why some traps served their purpose very well while others were practically useless. There seems no reason, for instance, why the two entrance traps fixed nearer the cement tank at the mosque should have taken no mosquitos at all, while the one further away (No. 6) collected many. The only conceivable suggestion is that mosquitos which entered this trap did not originate from the mosque at all. But in spite of very thorough searches for alternative breeding sites, no such places were found and captures made outside and just beside the three traps resulted in more being taken at trap No. 6 than at the others. The only difference in environment seemed to be that the entrance to trap No. 6 was in a more shaded position than those of the other two, as the palm-thatch roof of the adjacent house almost touched that of the one in which No. 6 was situated. It is just possible that mosquitos rested in this shade and thus found their way into the trap more easily, but some, at least, would have been expected to enter the other traps at the peak activity periods of early morning and dusk, when the question of the presence or absence of shade would not arise.

The activity rhythm.—In a review of all data collected from window traps, two periods—the early morning and late afternoon—are outstanding since they recur again and again whether males or females, flight, ovulation, feeding or fertilisation are being considered. These times are also conspicuous in biting catches outdoors in various situations and there seems little doubt that they form the prominent part of general activity rhythm. But in catches to demonstrate the biting-cycle, flight or dispersion, the interpretation of results must be based on the assumption that times of biting, flight, etc., may be influenced by conditions in the immediate vicinity. Thus, in adult captures where Africans were used as bait, whether conducted outside or in houses, it had been evident from the first that at the very start of a catch some females would almost invariably be taken in the first minute or two, quite irrespective of the time at which the catch started. There would be few or many depending presumably on the number in the vicinity which were ready to bite. Particularly was this noticeable in houses, and it is believed to be due to the sudden entry of the catchers into a confined space (a small room). Hungry females were thereby stimulated to feed, and after they had been captured there were left only those which had just emerged or for other reasons were not ready to bite. If, as was sometimes the case, the catch started during the night, it might account for the higher captures during these hours.

In biting catches outside, spatial considerations differ, but even here hungry females in the immediate vicinity would presumably feed at once and it would take time for others further off to locate the bait. Lumsden * has suggested that the lull following this initial activity might be due to the cessation of movement on the part of the catchers failing to attract the females.

Whatever the reason, this initial biting was so noticeable that it was thought its effect upon the true biting-cycle might be such as to jeopardise its validity, particularly when 24-hour catches always started at the same time. The biting catches in a house previously described strongly suggest this, but it had not been noticed by Mattingly in West Africa though both Haddow and Lumsden had been aware of it in the case of some other mosquitos during their work on the epidemiology of jungle yellow fever in Uganda. The latter workers had continued catches for a limited number of days, either getting settled a little before the catch was due to start and swatting mosquitos until the time came for the catch to begin (Haddow) or adding an extra few hours to the end of the catch and subsequently discarding the same number of hours at the beginning when analysing the data (Lumsden), but in the experiments at Kwa Shekh and Mombasa the longest catch extended over 24 hours only. However, it is felt that since they were carried out in a variety of situations over two years (in daylight catches almost daily for two years and eight months) such a long period would tend to even out any exceptional catches and produce perhaps a more accurate picture of activity than a continuous catch over a short period of days. Only if the mosquito population is very large does it seem that a continuous catch for a limited time will give accurate results and then only at the time of the year in which it is carried out.

---

* I am indebted to the workers mentioned in this and the following paragraph for their personal observations.

Further complex factors are involved in the movements of fertilised and unfertilised females. In the case of the former, the purpose of their egress from houses when they are fully gravid would seem to be only to lay eggs, yet opportunities for this appear to be no less favourable indoors where water is stored in numerous unprotected containers which are, in fact, used by *A. aegypti* for oviposition. There is little doubt that their exit is in some way connected with the activity rhythm because most gravid *A. aegypti* leave houses at the two peak periods of activity. However, there are a number of reasons which suggest the possible existence of two forms of *A. aegypti* on the Kenya coast, one of which may be solely house-frequenting while the other may exist outside but enters houses only for shelter or for a period of rest while the ovaries mature; but at present there is insufficient evidence to warrant a discussion on this question.

It may be opportune to mention at this point that the typical form of *A. aegypti* preponderates on the Kenya coast, but that pale specimens are also encountered. In fact all shades ranging from the darkest to the palest (var. *queenslandensis* (Theo.)?) are met with. Mattingly, in a personal communication, has made the interesting conjecture that pale forms may be less inclined to leave houses. Unfortunately, the suggestion was made after indoor captures had already been completed and the opportunity to carry out tests did not arise again.

Control.—The complete eradication of *A. aegypti* on this coast (where it seems to be far more prevalent than elsewhere in the Colony) would involve an undertaking of the greatest magnitude which, in the present circumstances, need not even be envisaged. Having regard, however, to the danger of the possible carriage by ships and aeroplanes of infected mosquitos to India and South Africa, where *A. aegypti* exists but where no cases of yellow fever have occurred, efforts at localised control in the seaports have, for the past decade, been undertaken with some measure of success; and since the experiments on larval development have shown that eight days is the normal minimum period required by adults to hatch from eggs, the weekly inspection cycle used in this control is probably adequate.

However, these efforts involve recurring expenditure which could only be obviated if the mosquito were eradicated. The investigations on control in houses undertaken at Kwa Shekh have shown that "house" control alone will never achieve the desired end since it is evident that even if the mosquitos can maintain themselves by living entirely indoors, as they will do in the laboratory, both males and females which originate from outside enter houses in which breeding has already been prevented. That these females lay eggs indoors seems almost certain, but window-trap catches suggest that a relatively small proportion of the population oviposits in houses. That they do so in significant numbers is, however, indicated by the fact that in the dry season, when larvae and adults disappear almost completely out-of-doors, breeding can be completely prevented in houses; but as soon as the rains occur and the outside mosquito population increases, so does breeding indoors become evident again.

It is also clear that *A. aegypti* will breed in houses in darkness. The Swahili dwellings have pit latrines in small windowless rooms in which water is stored in cement tanks and water pots for ablution purposes. These containers produce large numbers of *A. aegypti* at all times of the year and together with plant axils (Teesdale, 1941) may account to a large extent for the carry-over of adults from one wet season to another. Breeding in darkness does not apparently occur everywhere (Uganda Protectorate, 1938) and may be of considerable ecological significance on the coast.

In the laboratory, of course, *A. aegypti* will breed in complete darkness, but its presence in houses might result from a preference for oviposition in darkness rather than ability of the larvae to develop without light.

Summary.

Studies have been made of the bionomics and ecology of *Aëdes aegypti* (L.) entirely under natural conditions and in its natural habitats on the Kenya coast.

Development from egg to adult under conditions approximating as nearly as possible to those in nature took a minimum of eight days and a maximum of twenty-five.

Males were in excess of females, in the proportion seventeen to ten, from eggs hatched in natural breeding places.

Although the mosquito may be able to propagate in houses, adults from outside habitually enter premises. If this entry is for egg-laying, then eradication by domestic larval control alone, although reputedly achieved elsewhere, is not possible under conditions obtaining in the coastal belt of Kenya. Window-trap captures, however, indicate that the entry may not be for the purpose of egg-laying.

The seasonal reduction of both larvae and adults in houses during the hot, dry months of February and March is attributed to a combination of the absence of breeding places outside and the shorter life span of the mosquito at this time.

It is shown that both sexes enter and leave native huts throughout the 24-hour period, but the movement is confined almost wholly to the hours of daylight. The flight from houses is much reduced in the cool months (July and August). This corresponds with the season when most enter.

Most males enter between 9 a.m. and 1 p.m.—the time when least females do so. Both males and females leave houses at two peak times, 7 a.m. to 8 a.m. and 4 p.m. to 7 p.m. The proportion of males to females, both entering and leaving, is approximately one to three.

Those adults which enter huts probably do so for shelter and it is unlikely that their entrance is connected with feeding, mating or oviposition. There is some indication that only those females which have hatched indoors bite indoors.

Most of the females which enter huts have immature ovaries (Stage I), while most of those leaving are mature (Stage V). The majority of those with Stage I ovaries entered early in the morning and those at Stage V in the late afternoon. Out of a total of 201 Stage I females captured in window traps none had fed and all were unfertilised. Out-of-doors, 67 Stage I females captured biting were also unfertilised. Of 211 females captured in window traps and outside in other stages of ovarian development only three were apparently unfed and ten unfertilised. These facts indicate that pairing does not generally take place until after the female has fed.

A. aegypti will bite indoors and outside both by day and by night, but it is preponderantly diurnal in feeding, with two peak periods, the lesser between 10 a.m. and 1 p.m. and the greater from 4 p.m. to 7 p.m. The higher biting peak corresponds in time with that of the flight curve into and out of houses and is probably part of a general activity rhythm. The mosquito prefers biting in shade but will do so in bright sunlight.

The indications are that the range of flight is short but that dispersion is thorough. The female will reach considerable heights to feed (50 ft.) and oviposit (70 ft.), but its normal flight is near the ground.

The rôle of *A. aegypti* as a possible vector of yellow fever on the Kenya coast is discussed. Precipitin tests of the stomach contents of females show that there is another important host besides man, which is not included among the commoner domestic animals. Reasons are given for suggesting that lizards may be this host.

Acknowledgements.

My thanks are due to Dr. R. B. Heisch, Senior Parasitologist of the Division of Insect-Borne Diseases, Nairobi, for many helpful suggestions and interest shown throughout the course of these investigations.

I am also indebted to Sir Rickard Christophers, Mr. P. F. Mattingly of the British Museum (Natural History), Mr. C. B. Symes, O.B.E., Officer i/c Colonial Insecticides Research, Professor P. C. C. Garnham of the London School of Hygiene and Tropical Medicine and Dr. W. H. R. Lumsden of the Virus Institute, Entebbe, Uganda, all of whom have either kindly read through the drafts of this work or offered much valuable criticism and advice. I am also indebted to my wife who has given up much time to typing and preparing drafts.

Finally, I wish to record the debt owed to all those members of both African supervisory and subordinate staff who willingly gave up much of their time, over long periods, to uncongenial and monotonous tasks, but without whose help these investigations could not have been undertaken.

References.

Bailey, K. P. (1947). A preliminary note on the sylvan mosquitos of Gede.—E. Afr. med. J., **24**, pp. 38–41.

Buxton, P. A. & Hopkins, G. H. E. (1927). Researches in Polynesia & Melanesia. An account of investigations in Samoa, Tonga, the Ellice group, and the New Hebrides in 1924, 1925. Parts I–IV. . .—Mem. Lond. Sch. Hyg. trop. Med., no. 1, 260 pp.

Cardamatis, J. P. (1929). La dengue en Grèce.—Bull. Soc. Path. exot., **22**, pp. 272–292.

Christophers, S. R., Sinton, J. A. & Covell, G. (1936). How to do a malaria survey . . .—Hlth Bull., Simla, no. 14 (3rd edn.), 206 pp.

Davis, D. E. (1944). A comparison of mosquitoes captured with an avian bait at different vegetational levels.—Rev. Ent., Rio, **15**, pp. 209–215.

Drake-Brockman, R. E. (1913). Some notes on *Stegomyia fasciata* in the coast towns of British Somaliland.—J. Lond. Sch. trop. Med., **2**, pp. 166–169.

Garnham, P. C. C., Harper, J. O. & Highton, R. B. (1946). The mosquitos of the Kaimosi Forest, Kenya Colony, with special reference to yellow fever.—Bull. ent. Res., **36**, pp. 473–496.

Goeldi, A. E. (1905). Os mosquitos no Para.—Mem. Mus. Goeldi (paraense), **4**, 154 pp.

Gordon, R. M. (1922). Notes on the bionomics of *Stegomyia calopus*, Meigen, in Brazil. Part II.—Ann. trop. Med. Parasit., **16**, pp. 425–439.

Haddow, A. J. (1942). The mosquito fauna and climate of native huts at Kisumu, Kenya.—Bull. ent. Res., **33**, pp. 91–142.

HADDOW, A. J. (1945). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—Bull. ent. Res., **36**, pp. 33–73.

HADDOW, A. J. (1952). A review of the results of yellow fever protection-tests on the sera of primates from Kenya.—Ann. trop. Med. Parasit., **46**, pp. 135–143.

HADDOW, A. J., GILLETT, J. D. & HIGHTON, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate.—Bull. ent. Res., **37**, pp. 301–330.

HADDOW, A. J. & MAHAFFY, A. F. (1949). The mosquitoes of Bwamba County, Uganda. VII. Intensive catching on tree-platforms, with .further observations on *Aedes* (*Stegomyia*) *africanus*, Theobald.—Bull. ent. Res., **40**, pp. 169–178.

HADDOW, A. J., SMITHBURN, K. C., DICK, G. W. A., KITCHEN, S. F. & LUMSDEN, W. H. R. (1948). Implication of the mosquito *Aëdes* (*Stegomyia*) *africanus* Theobald in the forest cycle of yellow fever in Uganda.—Ann. trop. Med. Parasit., **42**, pp. 218–223.

HARRIS, W. V. (1942). Notes on Culicine mosquitos in Tanganyika Territory.—Bull. ent. Res., **33**, pp. 181–193.

HOCKING, K. S. & MACINNES, D. G. (1948). Notes on the bionomics of *Anopheles gambiae* and *A. funestus* in East Africa.—Bull. ent. Res., **39**, pp. 453–465.

HOWARD, L. O., DYAR, H. G. & KNAB, F. (1912). The mosquitoes of North and Central America and the West Indies. Vol. 1.—520 pp. Washington, D.C., Carnegie Inst.

JOHNSON, H. A. (1937). Notes on the continuous rearing of *Aëdes aegypti* in the laboratory.—Publ. Hlth Rep., **52**, pp. 1177–1179.

KENNEDY, J. S. (1942). On water-finding and oviposition by captured mosquitoes.—Bull. ent. Res., **32**, pp. 279–301.

KERR, J. A. (1933). Studies on the abundance, distribution and feeding habits of some West African mosquitos.—Bull. ent. Res., **24**, pp. 493–510.

LUMSDEN, W. H. R. (1952). The crepuscular biting activity of insects in the forest canopy in Bwamba, Uganda. A study in relation to the sylvan epidemiology of yellow fever.—Bull. ent. Res., **42**, pp. 721–760.

MACGREGOR, M. E. (1931). The nutrition of adult mosquitoes: preliminary contribution.—Trans. R. Soc. trop. Med. Hyg., **24**, pp. 465–472.

MAHAFFY, A. F., SMITHBURN, K. C., JACOBS, H. R. & GILLETT, J. D. (1942). Yellow fever in western Uganda.—Trans. R. Soc. trop. Med. Hyg., **36**, pp. 9–20.

MATTINGLY, P. F. (1949*a*). Studies on West African forest mosquitos. Part I. The seasonal distribution, biting cycle and vertical distribution of four of the principal species.—Bull. ent. Res., **40**, pp. 149–168.

MATTINGLY, P. F. (1949*b*). Studies on West African forest mosquitos. Part II. The less commonly occurring species.—Bull. ent. Res., **40**, pp. 387–402.

MATTINGLY, P. F. (1952). The sub-genus *Stegomyia* (Diptera, Culicidae) in the Ethiopian Region. I.—Bull. Brit. Mus. (nat. Hist.), Ent., **2**, pp. 235–304.

NUTTALL, G. H. F. & SHIPLEY, A. E. (1901). Studies in relation to malaria. II.—J. Hyg., Camb., **1**, pp. 45–77, 269–276, 451–484.

SEATON, D. R. & LUMSDEN, W. H. R. (1941). Observations on the effects of age, fertilization and light on biting by *Aëdes aegypti* (L.) in a controlled microclimate.—Ann. trop. Med. Parasit., **35,** pp. 23–36.

SHANNON, R. C., BURKE, A. W. & DAVIS, N. C. (1930). Observations on released *Stegomyia aegypti* (L.) with special reference to dispersion.—Amer. J. trop. Med., **10,** pp. 145–150.

SHANNON, R. C. & DAVIS, N. C. (1930). The flight of *Stegomyia aegypti* (L.).—Amer. J. trop. Med., **10,** pp. 151–156.

SHANNON, R. C. & PUTNAM, P. (1934). The biology of *Stegomyia* under laboratory conditions. I. The analysis of factors which influence larval development.—Proc. ent. Soc. Wash., **36,** pp. 185–216.

SMITHBURN, K. C., HADDOW, A. J. & LUMSDEN, W. H. R. (1949). An outbreak of sylvan yellow fever in Uganda with *Aëdes* (*Stegomyia*) *africanus* Theobald as principal vector and insect host of the virus.—Ann. trop. Med. Parasit., **43,** pp. 74–89.

SOPER, F. L., WILSON, D. B., LIMA, S. & SÁ ANTUNES, W. (1943). The organization of permanent nation-wide anti-*Aëdes aegypti* measures in Brazil.—137 pp. New York, Rockefeller Foundation.

TEESDALE, C. (1941). Pineapple and banana plants as sources of *Aëdes* mosquitoes.—E. Afr. med. J., **18,** pp. 260–267.

TOUMANOFF, C. (1949). L'hémophagie variée et l'activité reproductrice chez *Aedes aegypti* L. et *Aedes albopictus* Skuse.—Bull. Soc. Path. exot., **42,** pp. 466–470.

UGANDA PROTECTORATE. (1939). Report of the Entomologist.—Rep. med. Dep. Uganda, 1938, pp. 62–63.

WISEMAN, R. H., SYMES, C. B., MCMAHON, J. C. & TEESDALE, C. (1939). Report on a malaria survey of Mombasa.—60 pp. Nairobi, Govt. Printer.

WOKE, P. A. (1937*a*). Effects of various blood fractions on egg production of *Aëdes aegypti* Linn.—Amer. J. Hyg., **25,** pp. 372–380.

WOKE, P. A. (1937*b*). Comparative effects of the blood of different species of vertebrates on egg-production of *Aëdes aegypti* Linn.—Amer. J. trop. Med., **17,** pp. 729–745.

WOKE, P. A. (1937*c*). Cold-blooded vertebrates as hosts for *Aëdes aegypti* Linn.—J. Parasit., **23,** pp. 310–311.

YOUNG, C. J. (1922). Notes on the bionomics of *Stegomyia calopus*, Meigen, in Brazil. Part I. Preponderance of males in hatches.—Ann. trop. Med. Parasit., **16,** pp. 389–406.

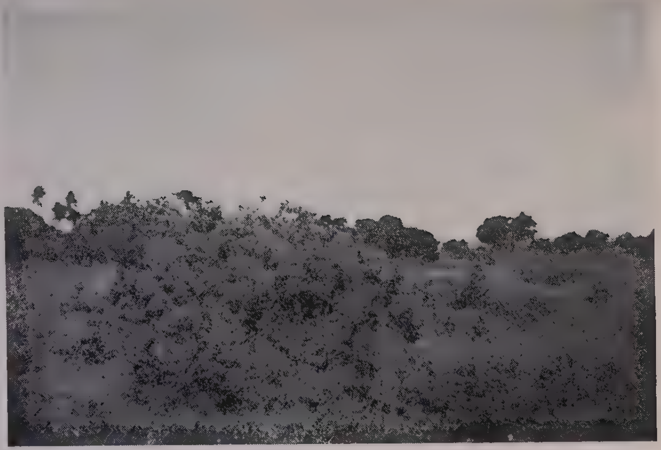


FIG. 1. On the edge of the coconut belt. More open country in the foreground; mangos, palms, etc., in the background.

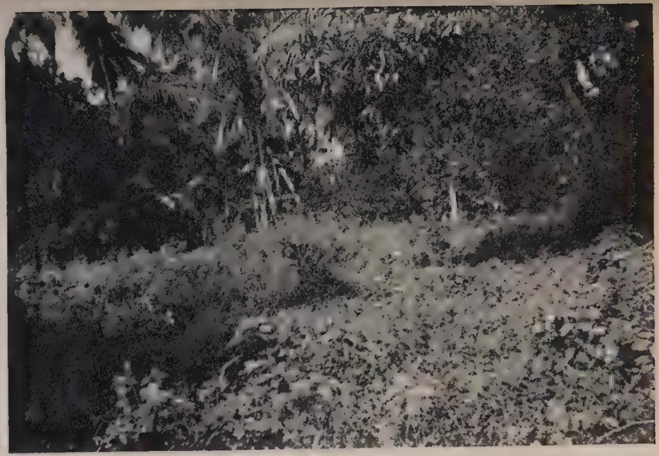


FIG. 2. Typical vegetation around Kwa Shekh. Amongst the trees are: Cashew nut (extreme left), bananas, coconut palms, mango (centre top), paw-paw and *Citrus* (right background).

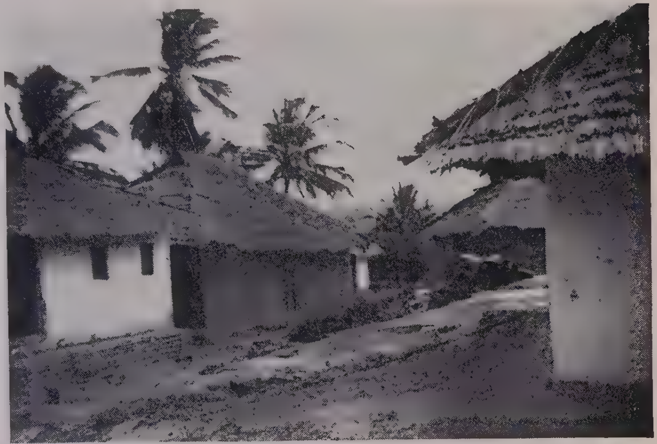


FIG. 3. A part of Kwa Shekh village showing coconut palms growing in and around the village.

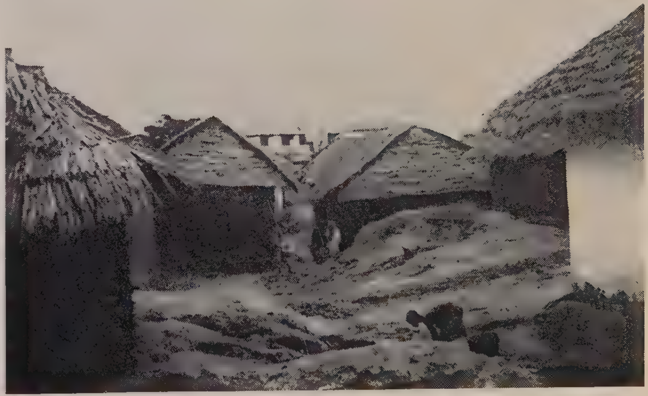


FIG. 4. A part of Jomvu village showing the absence of trees. The mosque in centre background.

A METHOD FOR CONTROLLED BREEDING OF COTTON STAINERS, *DYSDERCUS* SPP. (PYRRHOCORIDAE).

By Q. A. Geering

*Empire Cotton Growing Corporation, Cotton Research Station, Uganda.**

Cotton stainers, *Dysdercus* spp., are one of the most important groups of cotton pests, and have been studied intensively in the field. They are now being used more extensively as test insects for insecticide toxicology studies, and also for teaching purposes. Because of the wide interest now being shown in these insects, a brief description is given here of the technique employed at the Cotton Research Station in Uganda for breeding them on a large scale.

The maintenance of a stock of stainers in captivity is a relatively simple process and perhaps this is why only one reference is known, giving a very brief description of a method used (MacGill, 1935). A method frequently employed appears to be the use of a large wooden-framed cage which, in the tropics, is enclosed with mosquito screening and kept in an outdoor insectary. In order to maintain the stainers at a suitable temperature in England, such a cage can be enclosed with glass and heated by an electric light bulb. One such cage has been seen where the floor was covered with a deep litter of moist peat, providing an admirable environment for the development of eggs and first-instar nymphs. Stainers bred in captivity are, however, prone to disease and cannibalism, both of which are difficult to control in the conventional type of cage.

At the Cotton Research Station, stainers were required for insecticide studies, and for experiments to study the effect of different foods on the fertility and fecundity of adults, and the development of nymphs. For both purposes, it was essential that all the insect material should be of known age and parentage. Further, in order to produce a regular supply of insect material, it is necessary to maintain the breeding at maximum efficiency, which involves keeping a check on the fecundity of females, fertility of eggs and mortality during nymphal development. This means that oviposition, incubation of eggs and rearing of nymphs must proceed separately.

For the first and last of these processes, a standard type of cage was designed, which is illustrated in fig. 1. The cage is essentially a shallow, tin-plated cylinder, 10 in. in diameter by 5 in. high, open at the top and bottom. The floor and roof of the cage are provided by cotton cloth held in position by wire rings. The cages rest on wooden frames with 1-in. mesh chicken-wire, thus providing free ventilation, and the cloth cover is removed when changing the food or examining the colony. Within these cages, adult males and females are supplied daily with fresh cotton-seed soaked in water. Eggs are deposited freely on to the cloth floor of the cage. These are collected daily and incubated on moist filter paper in small glass dishes at 30°C. (86°F.), at which temperature they hatch after three days. The first-instar nymphs do not feed, and are kept in the same dishes at this temperature, in a saturated atmosphere, until they moult to the second instar in 2–3 days. The second-instar nymphs are then transferred to standard cages in groups of 150 and provided with fresh food daily, when they pass through the remaining three nymphal instars. Each cage of nymphs is provided with some loosely rolled corrugated paper, within which the nymphs are able to aggregate. Colonies of fifth-instar nymphs are supplied with a bundle of dry branching twigs, as they undergo their final moult more easily when they are able to suspend themselves from these.

---

* Now at School of Agriculture, University of Cambridge.

At one stage in the breeding work in Uganda, a disease developed progressively in all colonies, until the whole culture was killed off. This disease took the form of a deformation during the final moult, from fifth instar to adult: it varied in its effect from killing the adult before it had completely emerged, to causing a slight distortion of the hemelytra in the successfully moulted adult. Such individuals were either sterile, became egg-bound, or laid largely infertile eggs. Diseased and healthy specimens were sent to Professor E. A. Steinhaus of the University of California, who isolated three strains of gram-negative, lactose-fermenting bacteria. He reported that only one of these three strains was peculiar to the diseased specimens, and considered that it might even so be active only in a secondary capacity, and not necessarily cause the symptoms of disease described

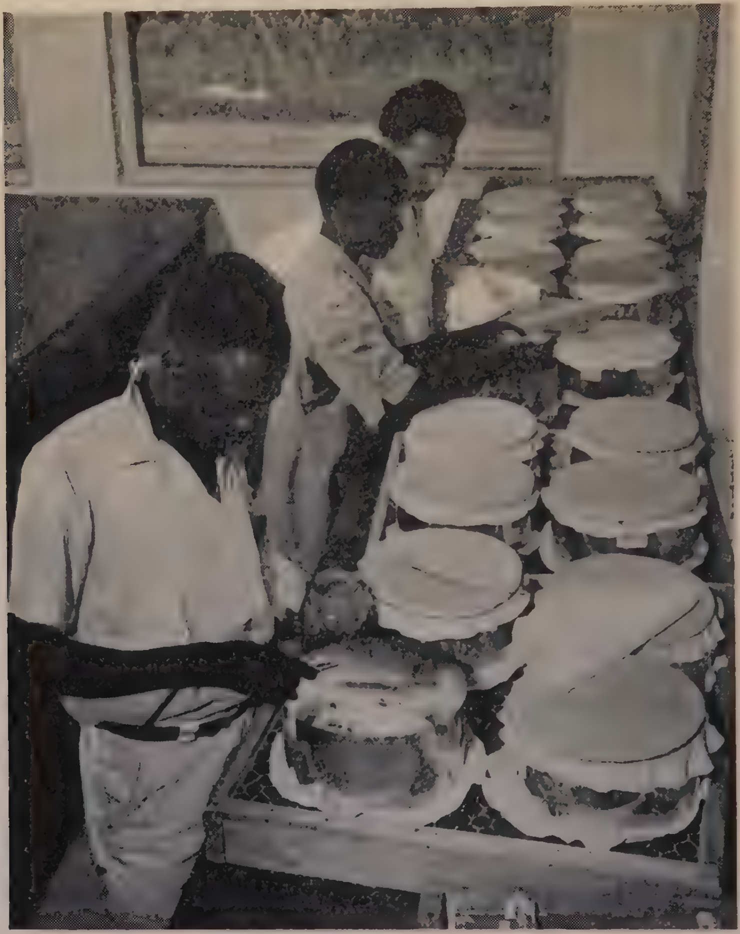


Fig. 1.—Arrangement of cage units for stainer breeding in the insectary, Cotton Research Station, Uganda. Bottom left, fresh cotton seed being supplied.

above. Without carrying out infectivity experiments to determine the exact cause of the disease, rigorous hygiene measures were then employed in Uganda, after re-starting the culture from a fresh collection of nymphs from the field. The same culture has since been going for two years, during which time the disease has appeared only once, in one cage, in which, as a precaution, the stainers were immediately destroyed. It seems very likely, therefore, that the disease is bacterial.

The particular advantages of the system of breeding described are as follows:—

(1) The unit is simple and cheap. The metal cylinders were purchased (made to specification) from a factory in East Africa for 9d. each. The arrangement of the cages shown in fig. 1 was used in an open-sided, roofed insectary at the Cotton Research Station in Uganda, where the mean daily maximum and minimum temperatures are 83° and 61°F., respectively. Under these conditions the life-cycle from egg to egg occupied 60 days. This period was reduced by incubating the eggs at 30°C., when the incubation period was shortened from ten days to three. For use in a temperate climate, it would be relatively simple to arrange these cages in drawer-like fashion in a heated room.

(2) Each cage unit can be dismantled and thoroughly cleaned and sterilised, the cloth covers being boiled and washed. Sterilisation of all other equipment is effected with a 0·1% solution of thymol. Fresh corrugated paper and fresh twigs are provided in each cage.

(3) The breeding procedure can be completely controlled, and by rearing nymphs of known origin in each cage the degree of inbreeding can be determined. In practice, eggs from each cage are collected and incubated separately, and when the second-instar nymphs are set out in fresh cages, they are mixed in approximately equal numbers from each parent cage. Four such parent cages, each containing about 100 adults, are used for egg-production over a period of three weeks, *i.e.*, covering the first three egg-batches. After the third batch, fecundity and fertility tend to fall off.

(4) By having the culture divided into units there is less chance of the whole culture being lost through disease or accident; if disease or cannibalism develops, or predatory ants gain access, any unit affected can be destroyed. Cannibalism can be eliminated by careful attention to the colonies; it is necessary each day to remove any dead individuals, which can be done when the food is changed.

The dimensions of the cylinder were selected so that the adults cannot fly out because their angle of take-off is less than the angle subtended by the height of the cage. Adults and larger nymphs can be prevented from crawling out by very lightly smearing the inner surface of the upper quarter of the cylinder with vaseline: this does not, however, confine second-instar nymphs, and for these a cloth cover is necessary. When the colonies were dying from disease the use of vaseline was discontinued and cloth covers were used throughout. If an antiseptic preparation could be used, a slippery barrier could safely be re-employed.

The author does not wish to claim sole credit for devising this simple cage. It was evolved after considerable discussion with Mr. E. O. Pearson, who had previously employed a similar technique for breeding stainers in South Africa and Nyasaland: it became apparent that all that is required for rearing this type of insect is a simple barrier for confining nymphs or adults, and the metal cylinder appeared to be the cheapest and most durable material for this purpose. The writer wishes to express appreciation to the Central Office of Information for permission to publish the accompanying photograph, taken by their representative on a visit to Uganda in 1951, and also to thank Professor Steinhaus for examining diseased stainers and allowing a report on his findings to be included in this note.

Summary.

A description is given of the method used for the large-scale breeding of cotton stainers (*Dysdercus* spp.) at the Cotton Research Station in Uganda. The method entails the use of a standard cage unit, consisting of a shallow tin cylinder with detachable cloth top and bottom. The advantages of this type of unit are outlined, with particular reference to control of disease and to the other hazards of large-scale breeding.

Reference.

MacGill, E. I. (1935). On the biology of *Dysdercus howardi*, Ballou (Hem.).—Bull. ent. Res., **26**, pp. 155–162.

FURTHER NOTES ON THE GEOGRAPHICAL DISTRIBUTION OF OLD WORLD SPECIES OF *ORNITHODOROS* (ACARINA).

By H. S. Leeson
London School of Hygiene and Tropical Medicine.

Since the publication of the previous paper (Leeson, 1953), additional information has been accumulated on the geographical distribution of some of the Old World ticks of the genus *Ornithodoros* and two new species (*zumpti* and *arenicolous*) have been described. Much of this additional matter has been communicated to me by correspondents who have been kind enough to give permission for its publication here. Their names are enclosed in brackets after the new data to indicate the source and to these workers I tender my sincere thanks. They are Dr. M. Baltazard, Teheran, Iran; Dr. J. Colas-Belcour, Paris, France; Mr. M. Crawford, Weybridge, England; Dr. G. E. Davis, Hamilton, U.S.A.; Dr. R. B. Heisch, Nairobi, Kenya; Dr. H. Hoogstraal, Cairo, Egypt; and Dr. J. Weiser, Prague, Czechoslovakia.

The following records should be added to those already given in the earlier list:—

arenicolous Hoogstraal, 1953.

This new species is of rare occurrence in widely scattered localities in littoral areas of the western and eastern deserts of Egypt (Hoogstraal).

capensis Neumann, 1901.

This tick has now been taken in New South Wales and Guam (Hoogstraal).

coniceps Canestrini, 1890.

Dr. G. Blanc has recently found this species in Morocco (Colas-Belcour).

delanoei Roubaud & Colas-Belcour, 1931.

Egypt (Davis; Hoogstraal).

erraticus (Lucas), 1846.

Turkey, near Syrian border (Hoogstraal).

foleyi Parrot, 1928.

Widely distributed locally in the eastern desert of Egypt near the Sudan border (Hoogstraal).

lahorensis Neumann, 1908.

On sheep in Macedonia (Weiser); received from Jugoslavia (Davis); Turkey, near Greek border (Hoogstraal).

salahi Hoogstraal, 1953.

Recently recorded from Jerusalem, Israel (Hoogstraal).

tartakovskyi Olenev, 1931.

Locality omitted from previous list, Meched, N.W. Persia (Baltazard & others, 1952) (Baltazard).

tholozani (Laboulbène & Mégnin), 1882.

Egypt, near Libyan border (Hoogstraal).

zumpti Heisch & Guggisberg, 1953.

This new species was described from specimens obtained from a burrow of the striped mouse (*Rhabdomys pumilio*) near Cathcart, Cape Province, South Africa (Heisch).

Apart from these new records, attention is drawn to the following comments on *Ornithodoros savignyi* (Audouin) 1826 :—

i. In the previous paper (Leeson, 1953), the first recording of *O. savignyi* in Ceylon was attributed to Brumpt (1936), but I omitted to mention that in his paper Brumpt acknowledged the receipt of the specimens from Mr. M. Crawford who was then the Government Veterinary Surgeon, Ceylon. An account of the original discovery of this tick in Ceylon, and its identification, is given by Crawford (1937).

ii. Also in my previous paper, the Belgian Congo was included among the records for *O. savignyi*. The Congo records were derived from Nuttall & others (1908–15) and have been quoted by many authors. It now seems that the existence of *O. savignyi* in the Congo must be regarded as at least uncertain, because the first reference to its occurrence in the Congo is attributed by Nuttall & others (1908–15) to Pocock (1900, page 49) and on that page there is no mention of the Congo, and also because the second reference quoted by Nuttall & others (1908–15), given as Pocock (1907), states merely that *O. savignyi* " has been recorded from . . . and the Congo " without any more detail. I have been unable to trace the origin of these Congo records and can only conclude that the references are erroneous; there seems now to be no explanation for the misquotations.

References.

BALTAZARD, M., BAHMANYAR, M., POURNAKI, R. & MOFIDI, C. (1952). Ann. Parasit. hum. comp., **27**, pp. 311–328.

BRUMPT, E. (1936). Ann. Parasit. hum. comp., **14**, pp. 640–646.

CRAWFORD, M. (1937). Adm. Rep. Dir. Agric. Ceylon, 1936, p. 75.

HEISCH, R. B. & GUGGISBERG, C. A. W. (1953). Parasitology, **43**, pp. 136–138.

HOOGSTRAAL, H. (1953*a*). J. Parasit., **39**, pp. 256–263.

HOOGSTRAAL, H. (1953*b*). J. Parasit., **39**, pp. 505–516.

LEESON, H. S. (1953). Bull. ent. Res., **44**, pp. 517–526.

NUTTALL, G. H. F., WARBURTON, C., COOPER, W. F. & ROBINSON, L. E. (1908–15). Ticks: a monograph of the Ixodoidea.—585 pp. Cambridge, Univ. Press.

POCOCK, R. I. (1900). Proc. zool. Soc. Lond., **1900**, pp. 48–63.

POCOCK, R. I. (1907). Ticks.—*In* Allbutt, T. C. & Rolleston, H. D. A system of medicine, **2**, pp. 187–203.

ROMAN, E. & NALIN, P. (1948). Ann. Parasit. hum. comp., **23**, pp. 214–219.

NOTES ON *PRISTIPHORA GLAUCA* BENSON.

By R. C. Kirkland and J. H. Styles E,H,U

During the course of field investigations into the larch-sawfly complex in Britain, a new larch-feeding species was taken. Adults and larvae were submitted to Mr. R. B. Benson of the British Museum (Natural History), whose examinations showed them to be of a hitherto undescribed species which he named *Pristiphora glauca* (Benson, 1954). The nominal characteristic of the species is the general blue-green body colour of the later-instar larvae, and Benson gave characters differentiating the adults from those of the closely allied *Pristiphora wesmaeli* (Tischb.).

Both the adult insects and the larvae bear a very marked resemblance to those of *P. wesmaeli*, and the larvae of both species feed mainly upon the new shoots of foliage within about ten feet of the ground, destroying the single needles from the tip of the shoot backwards, and sometimes continuing on to the dwarf shoots. Larvae of *P. wesmaeli* occur more frequently at the tips of the vigorous juvenile shoots, which grow almost vertically upwards and bear very succulent foliage; those of *P. glauca*, by comparison, feed upon the less vigorous new shoots of the lateral branches of older trees.

Larvae of all instars of *P. wesmaeli* are still abundant as late as the third week of August, whereas those of *P. glauca* have generally completed their development by the middle of June.

Although *P. glauca* cannot be an indigenous species in Britain, since larch is not native to this country, there is little evidence to indicate its distribution elsewhere except in Switzerland (Benson, *loc. cit.*), and it is probable that *P. glauca* has previously been confused with *P. wesmaeli.*

Life-cycle.

The following information is derived from the rearing of insects in captivity, and from specimens taken in the field for laboratory studies.

Both males and females are on the wing from the end of March until early May, the greatest number of emergences being recorded in mid-April. The eggs hatch from 14–21 days after oviposition, and the larvae complete their development in 28–35 days. During the fifth instar, larvae assume a pink colour. They then descend to the ground, where the cocoons are spun in the forest litter. There is only one generation each year.

The egg.

Average length of egg, 1·28 mm. (1·19–1·35 mm.).

Placed singly in slits cut in needles of young flushing larch shoots.

First-instar larva.

Average width of head capsule, 0·53 mm. (0·48–0·60 mm.). Average length of larva, 3·1 mm. (2·9–3·5 mm.).

Head brown with minute stout darker bristles; lower edges of frons darker, labrum with wide margin darker; antennae brown, antecoria lighter; ocelli and ocularia black. Thorax and abdomen light green, paler ventrally, with granular appearance due to presence of minute bristles. Thoracic legs light brown, coxae darker with black diagonal line. V-marking brown, distinct. Prolegs unicolorous with body; with darker fleck on anterior aspect. Apex of anal segment bearing group of dark bristles; other segments with dark bristles arranged in two indistinct transverse rows. Spiracles light brown.

Second-instar larva.

Average width of head capsule, 0·68 mm. (0·75–0·95 mm.). Average length of larva, 5·5 mm. (4·1–7·4 mm.).

Head darker brown than in first instar but otherwise similar.

Thorax and abdomen light green, paler ventrally, granular. Thoracic legs brown, coxae with black diagonal line. V-marking brown, distinct, anterior arm finer and darker. Prolegs unicolorous with body, with darker fleck on anterior aspect. Dark bristles present on apex of anal segment; on pre- and post-epipleurites, and forming two indistinct transverse rows on segments other than anal one. Spiracles light brown.

Third-instar larva.

Average width of head capsule, 1·03 mm. (1–1·15 mm.). Average length of larva, 7·5 mm. (4·1–9·6 mm.).

Head chestnut brown with short bristles; frons and labrum dark brown; antennae dark brown, antecoria paler; epicranial suture dark; ocelli and ocularia black.

Thorax and abdomen yellow green, granular. Thoracic legs light brown, with grey flecks, coxae darker with black diagonal line. V-marking brown, distinct, anterior arm darker. Prolegs unicolorous with body, with distinct fleck bearing bristles on anterior aspect. Dark flecks with bristles present on apex of anal segment, on pre- and post- epipleurites, and forming two distinct transverse rows on segments other than the anal one, and more pronounced anteriorly. Spiracles light brown.

Fourth-instar larva.

Average width of head capsule, 1·27 mm. (1·2–1·3 mm.). Average length of larva, 8·3 mm. (8–10 mm.).

Head with dark brown mosaic pattern, except for a buff coloured area on lower half of frons, extending laterally just below ocelli. Clypeus light brown, but labrum and mandibles chestnut brown. Antennae brown, antecoria lighter. Ocelli and ocularia black.

Dorsal surface of thorax and abdomen blue-green; with grey black granulation extending laterally, but finishing abruptly above the spiracles. Lateral and ventral surfaces pale green. Dorsally each segment bears two distinct transverse rows of black tubercles, from each of which arises a short black bristle. The dorsum of the anal segment has a triangular patch of these tubercles and bristles. There is a similar though variable grouping of black tubercles and bristles on the pre- and post- epipleurites.

Thoracic legs grey; though pigment is broken up giving a speckled appearance. The diagonal line on the coxae is no longer continuous. Tarsal claws brown. Prolegs unicolorous with ventral surface, with anterior grey fleck. Spiracles light brown.

Fifth-instar larva.

Average width of head capsule, 1·45 mm. (1·29–1·57 mm.). Average length of larva, 11·9 mm. (8–15 mm.).

Head with light brown mosaic pattern, though mid-dorsal region is black brown fading into surrounding region. Frons deep chestnut; with light dots in the top angle. Apex of clypeus brown. Labrum and mandibles black brown. Antennae brown; anterior lighter. Ocelli and ocularia black.

Dorsal surface of thorax and abdomen dark blue-green, with distinct black granulation extending to just above spiracles. Lateral and ventral surface pale green. The two transverse rows of black bristles and tubercles are present on each segment, while those on the pre- and post- epipleurites are more distinct, having larger basal areas of black pigmentation.

Thoracic legs are black, though pigment is still broken up. Tarsal claws brown. Prolegs unicolorous with ventral surface, grey fleck on anterior surface showing minute black bristles. Spiracles light brown (fig. 1).

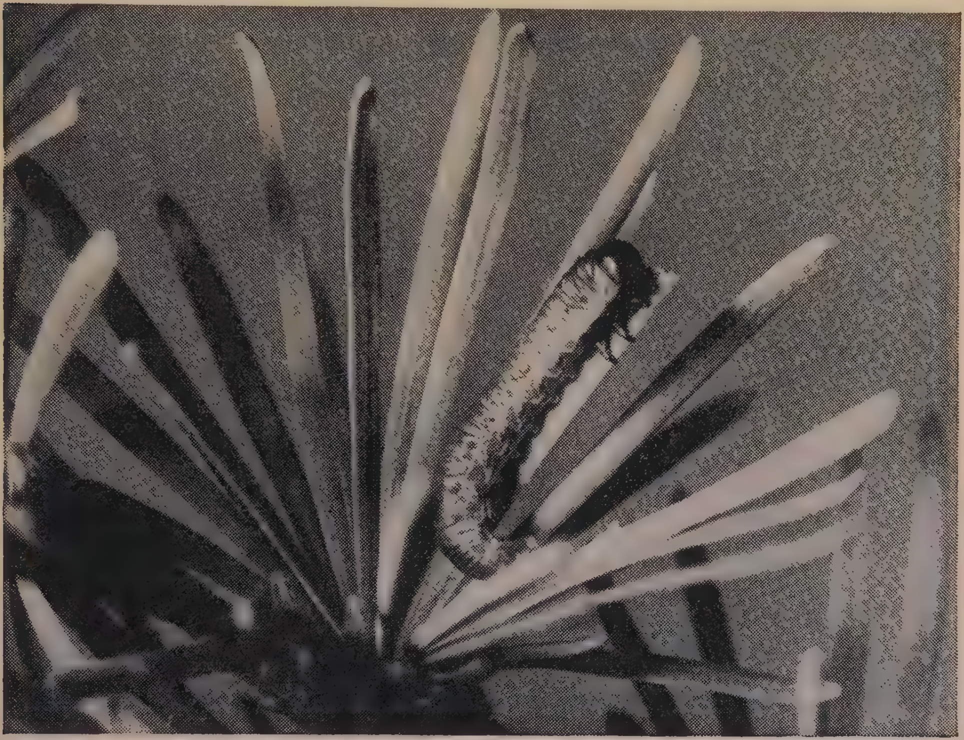


Fig. 1.—Fifth-instar larva of *Pristiphora glauca* Benson (× 5).

Distribution and Forest Status.

Owing to the restricted period of activity of this species, it was not possible to determine its complete distribution in Great Britain, but there are indications that, together with *Pachynematus imperfectus* (Zadd. & Brisch.), it is the least widespread of the larch sawflies. The greatest number of larvae were observed at Mortimer forest (Shropshire and Radnorshire), and Radnor forest (Radnorshire), a few specimens were also taken at Alice Holt forest (Surrey and Hampshire), and at Harling forest (Norfolk). Both European (*Larix decidua*) and Japanese (*Larix leptolepis*) larch were attacked. Injury to the trees does not assume serious proportions, and the winter buds are not affected.

Summary.

A new species of larch-feeding sawfly, *Pristiphora glauca* Benson, was first observed in 1950. The activities of this insect appear to be confined to the spring and early summer, and it would appear that it is one of the least widespread of the larch sawflies.

Notes on the biology of this species, including larval descriptions, are given, and field characteristics and distribution discussed. Differences in feeding habits from those of *Pristiphora wesmaeli* (Tischb.), with which it may be confused, are mentioned.

Acknowledgements.

The authors wish to thank those other members of the Entomology Section of the Forest Research Station, who have helped in the production of this article, and Mr. R. B. Benson of the British Museum (Natural History) for identification of the adults. This paper is published with the permission of the Forestry Commission.

Reference.

R.A.E.

Benson, R. B. (1954). Another new sawfly (Hym. Tenthredinidae) on larch in Britain.—Ent. mon. Mag., **90**, pp. 113–114.

ACARINE AND *NOSEMA* DISEASES OF HONEYBEES IN BRITAIN, 1925–47.

By Guy D. Morison, E. P. Jeffree, L. Murray and M. Delia Allen
Entomology and Bee Research Departments,
North of Scotland College of Agriculture, Aberdeen.

E.M.N

The very severe and rather sudden epidemic of a bee disease which was first reported in the Isle of Wight in 1905 and subsequently confirmed on the mainland, and which in several years did great damage to bee-keeping in Britain, has been a matter of interest to biologists as well as beekeepers.

Before 1919, when the causal organism was found to be the mite *Acarapis woodi* (Rennie) it had been supposed that the internal protozoan parasite *Nosema apis* might have been to some extent connected with the so-called "Isle of Wight Disease". But in the light of work by Rennie, White & Harvey (1921) it was soon accepted that, although *Nosema* disease was present in some cases, acarine disease was mainly responsible for the losses suffered.

Since this time, except for a more recent period studied at Rothamsted (Butler, 1945), it has not been clearly known whether the disease had remained static, or, if it had declined, to what extent. The present paper gives data for a long run of years that had not before been covered, and in addition affords some overlap with the more recent work, thus filling in a considerable part of what had previously been a field for speculation. The data for this period have been shown by Jeffree (1955) to be of key importance in establishing a broader theory of the action of temperature on acarine disease. This theory enables the very peculiar world distribution of the disease to be explained and also accounts for the fluctuations in its incidence during the years under consideration in this paper.

Information is also given on the course which *Nosema* disease followed for a number of years, and on the variations in the incidence of both diseases in different months of the year.

Method.

In the years 1925–47 inclusive, 9,929 samples of bees were examined for adult bee diseases and the results are presented in this paper. Of the samples examined, 4,470 were from England (with a few from Wales and Ireland) and 5,459 from Scotland. The numbers of samples examined each year varied between 394 and 73 from England, and 574 and 96 from Scotland. The sampling technique remained very closely the same throughout the period in question, and seems therefore unlikely to have affected the results. This claim rests on the following facts:—

1. All the examinations were carried out by the same microscopical technique and by one person only (G.D.M.).
2. In each year the mean number of bees examined per sample was comparable, varying between 13 and 17, and having an overall mean of 15.
3. All the samples were unsolicited, being sent in either for routine examination or because disease was suspected. Although this factor makes it probable that the proportion of diseased bees was somewhat higher than would have been found by random sampling, the relative incidence of disease in different years should not have been altered.

4. Samples from both England and Scotland were almost all sent in by post, and on a substantially similar basis, directly by the beekeepers themselves.

The data on seasonal variations in the incidence of acarine and *Nosema* diseases in Britain are calculated from the above figures for 1925–47, the total number of samples contributing to each monthly point on the graphs varying between 1,352 and 219.

Figures for the incidence of *Nosema* disease in the apiary of the Bee-keeping Research Department, North of Scotland College of Agriculture, between 1948 and 1953 were based on the systematic examination (by L.M.) of 867 samples, each consisting of about 20 bees. The number of colonies sampled averaged 38 each year, and the total number of samples in each quarter varied between 212 and 180. The colonies in question were not under any treatment for the disease.

Results.

The percentage incidences of *Nosema* and acarine diseases in samples of bees from England and Scotland between the years 1925 and 1947 are shown in fig. 1, where the data are grouped in yearly intervals running from May to April. It is apparent that *Nosema* was far less widespread than acarine disease in both countries. The incidence of acarine disease was also lower in England than in Scotland, while there is some suggestion of the reverse in the case of *Nosema*. The mean of the differences between the annual incidences of acarine disease in Scotland and England for the 22 years was 11·40 ± 2·43, which is statistically significant. For *Nosema* disease the corresponding mean was −1·47 ± 0·93, which is not significant.

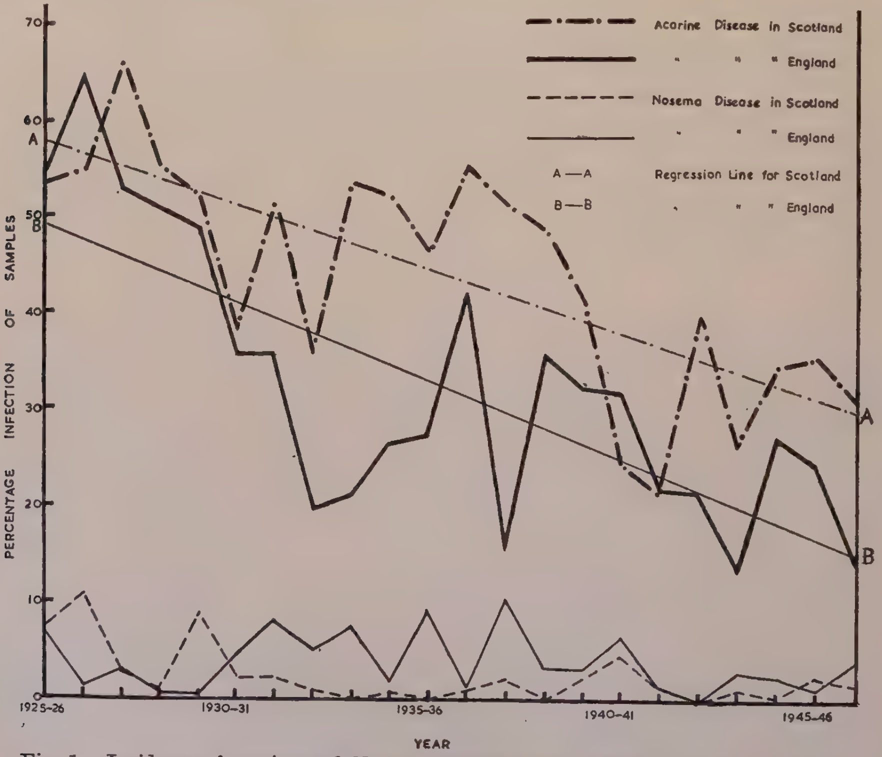


Fig. 1.—Incidence of acarine and *Nosema* diseases in England and Scotland (1925–47).

In addition to the wide fluctuations of acarine disease in England and Scotland seen in fig. 1, there is a clear indication of a fall in its incidence over the 22 years. The fall is, in fact, demonstrated in both countries when the appropriate regression lines (shown in fig. 1) are examined. These lines are represented by the following equations:—

1. England: $y = -1{\cdot}59x + 50{\cdot}83$
2. Scotland: $y = -1{\cdot}34x + 59{\cdot}44$

where x = year number (*i.e.*, 1 = 1925–26, 22 = 1946–47)
and y = % number of samples infested.

The standard errors of the regression coefficients are, respectively, 0·34 and 0·28. Thus there is no significant difference between the coefficients for the two countries, but each independently is significantly different from 0.

Information has also been obtained on the seasonal variations in the occurrence of acarine and *Nosema* diseases in Great Britain (figures for England and Scotland grouped together). Acarine disease was found to be least frequent in April, May and June; but *Nosema* disease followed a different course, showing its highest incidence in these three months and falling to a minimum in the autumn. Confirmation of this was obtained by the periodic examination of samples of bees from the apiary of the Beekeeping Research Department, in which *Nosema* was present between 1948 and 1953. These results are shown in figs. 2 and 3.

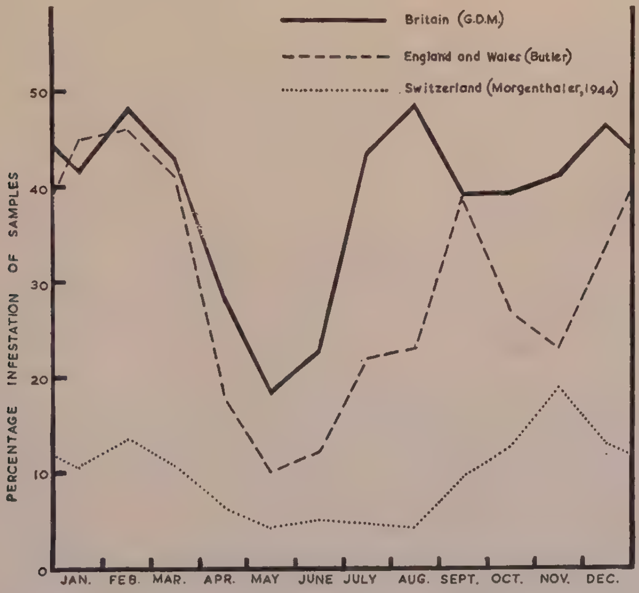


Fig. 2.—Seasonal variations in incidence of acarine disease.

Discussion.

Although acarine disease may well have been present in this country, and may have perhaps produced epidemics earlier than the beginning of the present century, for some years before 1905 it had not (at least apparently) been causing very notable damage. A major epidemic then started. Thus Butler (1945), drawing on Herrod-Hempsall and other sources, gives a picture of the disease having greatly increased in Britain between 1905 and 1918, when it was estimated that 90 per cent. of colonies were lost. Several methods were devised to control the disease and have been widely applied. None, however, seems to have been entirely successful, and it would, therefore, until recently have seemed a matter of debate whether the reduction in its incidence in both Scotland and England shown here had been due to control measures applied, or to changing methods of beekeeping, or to some other causes. One of us (Jeffree, 1955) has, however, now shown that there are definite relationships between summer and winter temperatures and acarine disease, and that when put in the appropriate mathematical form these relationships are in agreement with the otherwise surprising general decline in incidence seen in fig. 1, and also with the higher incidence of the disease in Scotland than in England. The relationships (which will be presented in detail in due course) are also in good general agreement with the rise in the incidence of acarine disease at the beginning of this century. On the other hand, *Nosema* disease (fig. 1) shows no indication of important long-term fluctuations or of ever reaching any very high general level in this country, and the above relationships for the two diseases provide further support for the main " Isle of Wight Disease " epidemic having been chiefly an epidemic of acarine and not of *Nosema* disease.

These new relationships between temperatures and acarine disease throw added interest on the course of the disease throughout an average year, and the

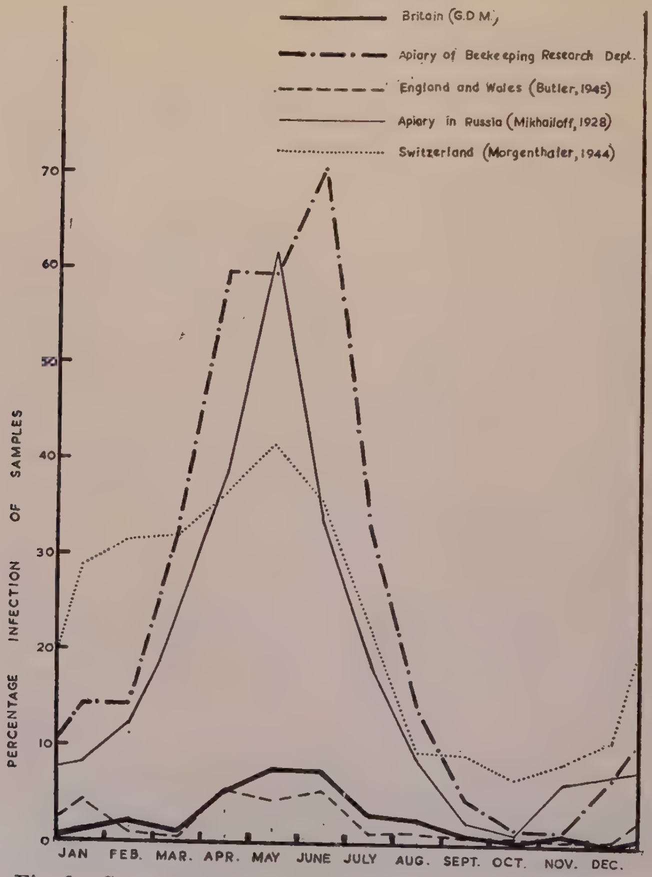


Fig. 3.—Seasonal variations in incidence of *Nosema* disease.

curves presented for *Nosema* disease are interesting as they afford an almost complete contrast to those for acarine disease. Each of these curves can form a basis for devising control measures for the respective diseases, and their elaboration for that reason becomes important.

There is some measure of agreement in the literature on the fluctuations of *Nosema* disease throughout the year. For example, the data of Butler (1945) and of Mikhailoff (1928) present a very similar picture to that described in this paper (see fig. 3). Morgenthaler's findings (1944) also show that the disease in Switzerland reaches its highest levels in April, May and June, though his figures for the winter months are relatively higher than those from other sources presented. It is uncertain whether it is justifiable to argue much from differences of this order, yet such an effect might not be unreasonable in a country where *Nosema* is five or six times more widespread than in Britain, this making it relatively less likely for the disease to disappear in September and October.

It is interesting to note, apart from the above slight discrepancy, that whether results for the incidence of *Nosema* were obtained by routine examination of samples from a wide area, as were those of Butler (England and Wales) and Morgenthaler, or from a single infected apiary (as in the case of Mikhailoff's figures for the Tula research apiary in Russia), the curves for the incidence of the disease run roughly parallel to one another. This similarity would appear to indicate that the results of the examination of samples sent in by beekeepers usually give a fairly reliable estimate of the actual fluctuations of this disease in individual colonies. Morgenthaler (1939) also stated this opinion.

Morgenthaler (1939) further pointed to the close parallel between the incidence of the disease and egg-laying, and discussed this in relation to length of life of the bee and in relation to the temperature of the brood nest. Jeffree (1949) argued that dysentery-stained combs are the probable cause of the parallel. The combs beneath the cluster become stained with material containing *Nosema* spores during late winter. Such spores will be picked up by the bees as the brood nest expands downwards over the comb, and this will go on so long, approximately, as the brood nest is expanding. Subsequently, however, the frequency with which new areas of staining are brought within the cluster is far less, and the disease begins to clear up. The results of Bailey (1953) indicated that transmission of the disease from diseased to healthy bees virtually ceased during the flying season, and that the primary means of transmission of the disease from year to year was comb which had been soiled by excreta during the winter. He obtained reduced infection by separating bees from stained combs.

Concerning acarine incidence, the figures published by Butler (1945) support those given here, particularly in the first half of the year (see fig. 2). Morgenthaler (1932 and 1939) believed that the disease fluctuated very little during the year in Switzerland, variations being due rather to the method of sampling. The graphs presented in his own papers, however (1939 and 1944), do not seem to be in a form either to substantiate or refute this view, since the monthly percentages he has used have not been obtained from division of the total number of samples received in each month, but by the total number of diseased samples throughout the twelve months. This quite different method of calculation contributes very materially to the different shapes of his graphs, and indeed also to the conclusions he has drawn from them. In fig. 2, we have re-plotted his data in the form given in column 4 of his table 4 (Morgenthaler, 1944, p. 314), that is, in the same form as that in which Butler's and Morison's results are presented, and the fluctuation of the disease in Switzerland, thus shown, is then similar in general trend to that in Britain.

Butler properly argued that various factors concerning the sampling technique might have affected the Rothamsted results, and as such factors apply equally to G.D.M.'s figures, it is still not possible to say at all definitely that the latter represent the absolute fluctuations of acarine disease throughout the year. The chief disturbing factor would arise from beekeepers observing crawling bees or other signs of the disease in one or more particular months, and consequently sending in an artificially high proportion of diseased samples in those months. Morgenthaler (1932), however, in a 10-year survey, found that approximately 90 per cent. of the samples found to be infested with acarine disease were sent in as routine samples, and only approximately 10 per cent. originated from beekeepers who had suspected disease. Of that 10 per cent., many were sent in during March, but the effect of these was not sufficient to contribute a major distortion of his curve obtained for all samples. The graphs for Britain are likely also to be a little distorted from such causes, but the main trends are, nevertheless, probably real. Further, the fact referred to above, that *Nosema* curves obtained in two different ways are so similar, would seem to strengthen the likelihood that the true acarine disease curve in Britain is basically of the shape given; and unpublished observations in this laboratory give support also to this view. If this is the case, the shape could well be related to the length of life of the bee, which is much greater in winter than in summer. Migration of mites from infested bees cannot take place to any major extent during the earlier part of the life of a bee, and any reduction in the mean age of a colony would therefore bring a corresponding decrease in the number of migrating mites. From this hypothesis it would be expected that the incidence of acarine disease would fall in the months when bee activity is at its highest and the average age of the bees is lowest (approximately the months when much brood is being reared) and would rise in times of inactivity where the average became higher (particularly, that is, in the winter months). Thus the same causal mechanism which Jeffree (1955) has suggested as reducing the overall incidence of acarine disease in sequences of years with high summer temperatures would here be the cause of the normal lowering of incidence of the disease in the summer months.

Summary.

Between 1925 and 1947, 9,929 samples of bees from Great Britain were examined for acarine and *Nosema* diseases. There was a significantly lower incidence of acarine disease in English samples than in Scottish ones, but a somewhat higher incidence of *Nosema* disease in England than in Scotland was not significant. A decrease in the incidence of acarine disease over the 22 years was highly significant in both England and Scotland, although the rate of decrease was not significantly different between the two countries.

The average incidence of acarine disease during each month of the year was at its lowest in April, May and June, while *Nosema* disease reached its maximum in these three months and fell to a minimum in the autumn. Data on the seasonal incidence of *Nosema* disease in an apiary in Scotland between 1948 and 1953 show a similar distribution to that for Great Britain. Results on the incidence of both diseases throughout the year are compared with those of other authors, and possible reasons for the seasonal fluctuations are discussed.

References.

BAILEY, L. (1953). The transmission of Nosema disease.—Bee World, **34**, pp. 171–172.

BUTLER, C. G. (1945). The incidence and distribution of some diseases of the adult honeybee (*Apis mellifera* L.) in England and Wales.—Ann. appl. Biol., **32**, pp. 344–351.

JEFFREE, E. P. (1949). Nosema and wintering.—Scot. Beekeep., **25**, pp. 189–191.

JEFFREE, E. P. (1955). Acarine disease of the honeybee and temperature.—Nature, Lond., **175**, p. 91.

MIKHAILOFF, A. S. (1928). Nosema an der Tulaer Versuchsstation für Bienenzucht.—Arch. Bienenk., **9**, pp. 89–114.

MORGENTHALER, O. (1932). Ein Jahrzehnt Milbenkrankheit der Honigbiene.—Z. angew. Ent., **19**, pp. 449–489.

MORGENTHALER, O. (1939). Die ansteckende Frühjahrsschwindsucht (Nosema-Amöben-Infektion) der Bienen.—Schweiz. Bienenztg, **62**, pp. 86–92, 154–162, 205–215.

MORGENTHALER, O. (1944). Das jahreszeitliche Auftreten der Bienenseuchen.—Schweiz. Bienenztg, Beih. 7 (Bd. 1), pp. 285–336.

RENNIE, J., WHITE, P. B. & HARVEY, E. J. (1921). Isle of Wight disease in hive bees. (1) The etiology of the disease.—Trans. roy. Soc. Edinb., **52**, pp. 737–754.

OBSERVATIONS ON THE BITING-HABITS OF AFRICAN MOSQUITOS IN THE GENUS *ERETMAPODITES* THEOBALD.

By A. J. Haddow

Virus Research Institute, Entebbe, Uganda.

The purpose of this paper is to describe the biting-behaviour of mosquitos in the genus *Eretmapodites* Theobald as shown by various series of 24-hour catches with human bait carried out in two Uganda localities between 1942 and 1948. The areas concerned are Bwamba County, heavily forested country on the borders of the Belgian Congo, which has been described elsewhere (Haddow, 1945*a*) and the Entebbe neighbourhood on the northern shore of Lake Victoria. Around Entebbe much of the country is occupied by mixed cultivation and open grassland, but there are also numerous small strips and patches of second-growth forest, particularly along the shores of the lake and its fringing swamps.

The species referred to in this paper are the following:—

Eretmapodites chrysogaster Grah.
,, *intermedius* Edw.
,, *mahaffyi* van Som.
,, *haddowi* van Som.
,, *harperi* van Som.
,, *semisimplicipes* Edw.
,, *gilletti* van Som.
,, *grahami* Edw.

Eretmapodites inornatus Newst.
,, *penicillatus* Edw.
,, *tonsus* Edw.
,, *quinquevittatus* Theo.
,, *ferox* Haddow
,, *oedipodius* subsp. *parvipluma* Edw.
,, *leucopus* subsp. *productus* Edw.

In a recent paper (Haddow, 1954) the writer has discussed the methods he has used in making 24-hour catches, and also the interpretation of their results. Reference should be made to the same paper for details of the various series concerned, as here only the briefest summary can be given. It should be noted that in both areas the catches were well distributed throughout the year. The series concerned were as follows:—

(a) Fifteen catches in forest and fifteen in banana plantations, all at ground level, Bwamba (Haddow, 1945*b*).

(b) Ten catches in a banana plantation in Bwamba at four levels simultaneously—ground level, 6, 12 and 18 feet (Haddow, 1945*c*).

(c) Twenty catches in forest at Mongiro, Bwamba, at four levels simultaneously—ground level, 16, 31 and 54 feet, and twenty catches in forest at Mamirimiri, Bwamba, at five levels simultaneously—ground level, 22, 44, 58 and 82 feet (Haddow, Gillett & Highton, 1947).

(d) Two hundred and forty catches made in Bwamba (40 localities) at ground level and in the forest canopy simultaneously (the "Bwamba Tree Survey").

(e) Thirty five catches made in two localities near Entebbe (7 stations) at ground level, understorey level and canopy level simultaneously (the "Entebbe Tree Survey") and with these, five catches in a banana plantation beside one of the forest stations.

The total numbers of *Eretmapodites* spp. taken in these series are shown in Table I.

In the entire sample—1,263 mosquitos—only four were taken biting above ground level (one *E. chrysogaster* gp. at 6 feet, one *E. ferox* at 16 feet and one at 31 feet, and one *E. oedipodius* subsp. *parvipluma* at 27 feet). From this it is obvious that these mosquitos are not deflected from their ground level biting-habit by the presence of units catching above. Thus it is felt that, in the case of this particular genus, all the Bwamba series can legitimately be combined and all the Entebbe series likewise.

This small, exclusively African, genus shows rather remarkable uniformity in behaviour and habitat and, generally speaking, the members show an all-over resemblance closer than that found in many African subgenera. At the same time, they are very distinct from all other Ethiopian mosquitos, though they resemble rather closely the oriental genus *Armigeres* (which is also rather similar in habits, behaviour and breeding places). All breed in small natural containers such as plant axils, tree holes, leaf pools and snail-shells, or occasionally in artificial containers. All the larvae so far studied in detail have proved to be facultative predators (Haddow, 1946). The adults frequent fairly dense shade, such as is provided by forest or by banana or other plantations, and the writer has never taken a specimen in a hut or house. All bite man readily, mainly by day and, as will be shown below, most biting occurs very close to the ground, almost entirely below the knee. This applies to all the species known to the writer. The approach to the bait is a visual one, direct and swift and (for some reason not understood) feeding is often interrupted, a given mosquito often returning twice or three times to the host before its blood-meal is complete.

TABLE I.

All species of *Eretmapodites* taken in 24-hour catches, 1942–48, totals.

Species or group	*E. chrysogaster* gp.	*E. inornatus* gp.	*E. ferox*	*E. oedipodius* ssp. *parvipluma*	*E. leucopus* ssp. *productus*	Totals
Bwamba						
15 original forest catches	58	—	25	—	—	**83**
15 original plantation catches	7	—	3	—	2	**12**
10 stratified plantation catches	3	—	—	—	—	**3**
20 stratified catches, Mongiro	12	3	3	—	—	**18**
20 stratified catches, Mamirimiri	2	—	—	—	—	**2**
240 stratified catches (Bwamba Tree Survey) ..	331	55	60	1	3	**450**
Subtotals	**413**	**58**	**91**	**1**	**5**	**568**
Entebbe area						
35 stratified catches (Entebbe Tree Survey) ..	462	—	—	224	—	**686**
5 plantation catches	8	—	—	1	—	**9**
Subtotals	**470**	—	—	**225**	—	**695**
Grand totals	**883**	**58**	**91**	**226**	**5**	**1263**

The genus first attracted attention when it was shown by Bauer (1928) that *E. chrysogaster* can transmit yellow fever virus under laboratory conditions. Subsequently Kerr (1933) contributed the first account of the biting-habits, but generally speaking very little work on this genus was undertaken until the taxonomic situation was cleared up by Edwards (1941) in his book on the Culicines of the Ethiopian Region. Subsequently the writer and others published brief accounts of the biting-habits (Haddow, 1945*b*; Haddow, Gillett & Highton, 1947) and at another stage the writer published a taxonomic paper in which descriptions of unknown stages and a new species were given, and in which attention was drawn to the predatory nature of the larvae (Haddow, 1946). Subsequently, van Someren (1949) described other new species of the *E. chrysogaster* group from Uganda. In Kenya, Garnham, Harper & Highton (1946) discussed larval habitats and gave notes on adult habits, and van Someren (1947) described a new species. More recently, Hoogstraal & Knight (1951) have given an account of a form from the Sudan.

During the same period, isolations of Rift Valley fever virus were made from three mixed lots of *Eretmapodites* in Uganda (Smithburn, Haddow & Gillett, 1948) and it was shown that members of the *E. chrysogaster* group could transmit the virus under laboratory conditions (Smithburn, Haddow & Lumsden, 1949). On the other side of the continent a virus at first known as Kumba virus was isolated from *E. grahami* in Cameroon (Macnamara, 1953). Subsequently it was shown that this agent was a strain of Semliki Forest virus—an agent originally isolated from mosquitos of the genus *Aëdes* in Uganda (Smithburn & Haddow, 1944).

Enough has been said to show that the mosquitos of this genus form an interesting and compact group, and further, that they may prove to be of importance in relation to the virus diseases of man and animals. The biting-cycles may now be discussed. The main results are shown in Table II. For reasons explained elsewhere (Haddow, 1954) the geometric mean (M_G) as modified by Williams (1937) is used wherever a measure of the central tendency is required. In most cases the geometric mean, worked out to three decimal places, has been multiplied by one thousand to give integer numbers (1000 M_G) more compact for tabulation. Thus 0·025 becomes 25.

The **Eretmapodites chrysogaster** group.

The members of this taxonomically difficult group are by far the most abundant and the most widely distributed of the genus in Uganda. Unfortunately, it is impossible to distinguish the females of the different species with certainty, and in most cases the dissection of terminalia is necessary for the reliable identification of the males. It is not possible, therefore, to discuss the behaviour of each species by itself, and thus there is inherent difficulty in the interpretation of the results. What may be said, however, is that in the areas under discussion (at least in the forest) *E. chrysogaster*, *sens. str.*, predominates. At Entebbe, *E. intermedius* is known to be present, but scarce. Thus dissection of a series of 40 wild-caught males and 48 males reared from the eggs of separate wild-caught females revealed only three *E. intermedius* among 85 *E. chrysogaster* (Smithburn, Haddow & Lumsden, 1949). In Bwamba, both *E. intermedius* and *E. semisimplicipes* are known to be present, as also are five rare species—*E. mahaffyi*, *E. haddowi*, *E. harperi*, *E. gilletti* and *E. grahami*. Here again however, the writer's experience, based on considerable numbers of dissections of wild-caught males and of males reared from larvae, is that *E. chrysogaster* is by far the commonest species. Certainly this applies in the case of males reared from females taken biting man. This point is one of importance, as it will be shown below that the biting-behaviour in Bwamba shows quite different characteristics from that observed at Entebbe. While this could be attributed to differences in the make-up of the group in the two areas, this is not thought to be the explanation, for reasons which will appear below.

When the figures for the entire Entebbe series are considered (Table II & fig. 1), it at once becomes apparent that the biting-cycle is a diurnal one, showing

TABLE II.

The biting-cycles of *Eretmapodites* spp. in Bwamba and the Entebbe area.

Species or group	Hour	Night								Day								Night								
		00–01	01–02	02–03	03–04	04–05	05–06	06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	Totals
E. chrysogaster gp. (Entebbe)	Arithmetic totals	0	1	0	0	0	1	19	17	17	31	27	18	12	15	25	29	96	142	17	3	0	0	0	0	470
	1000 M_G	0	17	0	0	0	17	244	280	296	362	315	272	200	159	289	319	879	1860	248	53	0	0	0	0	—
	M_G as percent.	0·0	0·3	0·0	0·0	0·0	0·3	4·2	4·8	5·1	6·2	5·4	4·7	3·4	2·7	5·0	5·5	15·1	32·0	4·3	0·9	0·0	0·0	0·0	0·0	99·9
E. chrysogaster gp. (Bwamba)	Arithmetic totals	7	5	9	9	5	10	25	25	21	24	36	23	18	20	35	29	24	38	13	14	4	6	7	6	413
	1000 M_G	34	27	49	41	23	52	132	124	120	129	166	120	101	96	188	178	138	190	76	59	19	27	27	29	—
	M_G as percent.	1·6	1·3	2·3	1·9	1·0	2·4	6·2	5·8	5·6	6·0	7·7	5·6	4·7	4·4	8·8	8·3	6·4	8·9	3·5	2·7	0·9	1·3	1·3	1·4	100·0
E. oedipodius subsp. *parvipluma* (Entebbe)	Arithmetic totals	2	0	0	0	0	0	12	7	11	16	9	9	3	9	11	23	47	57	9	0	0	0	0	0	225
	1000 M_G	35	0	0	0	0	0	175	96	180	234	140	160	53	160	145	327	620	897	140	0	0	0	0	0	—
	M_G as percent.	1·0	0·0	0·0	0·0	0·0	0·0	5·2	2·9	5·4	7·0	4·2	4·8	1·6	4·8	4·3	9·7	18·4	26·6	4·2	0·0	0·0	0·0	0·0	0·0	100·1
E. ferox (Bwamba)	Arithmetic totals	0	2	3	0	0	1	4	8	4	5	5	8	7	7	8	7	8	5	2	1	1	1	2	2	91
	1000 M_G	0	25	39	0	0	13	52	95	52	65	65	100	86	91	100	91	106	65	25	13	13	13	21	25	—
	M_G as percent.	0·0	2·2	3·4	0·0	0·0	1·1	4·5	8·2	4·5	5·6	5·6	8·7	7·4	7·9	8·7	7·9	9·2	5·6	2·2	1·1	1·1	1·1	1·8	2·2	100·0
E. inornatus gp. (Bwamba)	Arithmetic totals	3	0	0	3	2	2	2	6	4	4	4	3	1	1	0	1	4	5	3	2	2	0	4	2	58
	1000 M_G	104	0	0	104	68	68	68	202	140	140	140	104	34	34	0	34	126	179	104	54	68	0	126	68	—
	M_G as percent.	5·3	0·0	0·0	5·3	3·5	3·5	3·5	10·3	7·1	7·1	7·1	5·3	1·7	1·7	0·0	1·7	6·4	9·1	5·3	2·7	3·5	0·0	6·4	3·5	100·0
All species collectively (Entebbe)	Arithmetic totals	2	1	0	0	0	1	31	24	28	47	36	27	15	24	36	52	143	199	26	3	0	0	0	0	695
	1000 M_G	35	17	0	0	0	17	424	363	476	555	420	449	265	305	368	582	1441	2776	414	53	0	0	0	0	—
	M_G as percent.	0·4	0·2	0·0	0·0	0·0	0·2	4·7	4·1	5·3	6·2	4·7	5·0	3·0	3·4	4·1	6·5	16·1	31·0	4·6	0·6	0·0	0·0	0·0	0·0	100·1
All species collectively (Bwamba)	Arithmetic totals	10	7	12	12	7	14	31	40	30	34	45	34	27	28	43	37	36	49	18	17	7	7	13	10	568
	1000 M_G	40	32	55	45	24	57	132	148	131	149	171	152	127	113	187	185	173	205	144	55	28	28	40	39	—
	M_G as percent.	1·6	1·3	2·2	1·8	1·0	2·3	5·4	6·0	5·3	6·1	7·0	6·2	5·2	4·6	7·6	7·5	7·0	8·3	5·9	2·2	1·1	1·1	1·6	1·6	99·9

a distinct rise of activity in the period two hours before sunset, and continuing to form a very pronounced peak in the hour before sunset. When the crude figures are examined, it is found that 142 (30%) of the total 470 specimens were taken in the hour before sunset, while in the two-hour period preceding sunset 238 specimens (51% of the total catch) were taken. These percentages are of course slightly different from those obtained when the geometric mean is used, as in Table II. When, however, the Bwamba figures (Table II & fig. 1) are examined it is obvious that while in that area the cycle is diurnal, there are no marked peaks of activity at any time. In Bwamba, the fact that higher numbers were taken biting by night than at Entebbe was almost entirely due to one or two exceptional catch results.

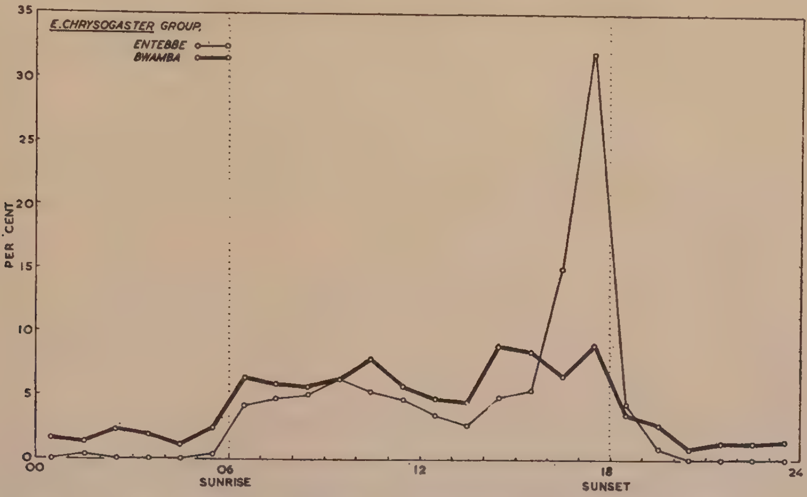


Fig. 1.—The biting-cycle of the *E. chrysogaster* group. The figures are geometric means. They have been reduced to a percentage basis to facilitate comparison with the other graphs.

In a recent paper Lumsden (1952) discussed the post-sunset wave of activity which occurs in species such as *Aëdes* (*Stegomyia*) *africanus* (Theo.). He suggested that in the case of a small-container breeder, where the total available larval breeding places are quite limited at all times, females might be rather long-lived, with numerous ovarian cycles, and that the population would contain a fairly high percentage of the older females. These, inhibited by light from biting, would build up during the day into a large group ready to bite immediately light conditions became favourable after sunset, thus forming the major post-sunset wave of activity characteristic of this species. The smaller numbers biting at later hours during the night were made up, he suggested, of young females biting for the first time. While this view may well be true of *A. africanus*, the writer (1954) has contested its general application. He pointed out that in the case of a small-container breeder inhibited not by light but by darkness there should be—if Lumsden's hypothesis is correct—a major wave of activity just after sunrise with much reduced activity thereafter. Even admitting that the low temperature after sunrise might be inimical to biting-activity, the wave should occur later in the morning. In discussing this point an example was given, namely the biting-behaviour of the *E. chrysogaster* group at Zika (part of the Entebbe Tree Survey), and this sample showed that the wave did not occur till just before sunset—*i.e.*, at the other end of the period of active biting. At that time the Bwamba sample had not been worked out but, since it has, it strengthens the writer's opinion and now it seems obvious, in view of the divergence of behaviour in the two areas, that no single explanation can hold good and that some more complex explanation than that advanced by Lumsden must be sought.

When the figures are examined in detail, it is found that biting may begin at any hour during the day and that there are even a few days on which no biting occurred except at night (though in this latter case the numbers are always very small—one or two mosquitos at the most in any given case). Following this lead, the figures for the important diurnal part of the cycle have been further analysed in Table III. Here the days have been sorted into groups, according to the time at which biting began. From these figures, the fundamental nature of the difference between the behaviour in the two areas becomes still more apparent. Thus, in Entebbe, no matter at what time biting began, there was a strong tendency for the highest numbers to be taken in the hour before sunset. In Bwamba, on the other hand, no matter when biting began the highest numbers were taken in the first hour of biting-activity. These facts are well brought out by the following figures, extracted from Table III.

Locality	Percentage of the total diurnal yield taken in the first hour of biting	Percentage of the total diurnal yield taken in the hour before sunset
Entebbe	12	32
Bwamba	40	12

It will be noted that the one set of figures is almost the reverse of the other.

With reference to the fact that the *E. chrysogaster* group bites a standing bait almost entirely below the knee, an experiment was carried out at Entebbe to determine whether this part of the body was specially preferred, or whether the preference was for a particular level just above the forest floor. In this experiment a totally unclothed bait stood and lay alternately for five-minute periods to a total of 3½ hours. The numbers of *E. chrysogaster* group taken biting were as follows:—

	Bait standing	Bait lying
Above the nipple line	0	17 (15%)
Nipple line to hip joint	0	49 (45%)
Hip joint to knee	8 (2%)	36 (33%)
Below the knee	327 (98%)	8 (7%)
Total	335	110

From these figures it is obvious that the mosquitos of this group do not specially prefer to bite the leg, but do prefer a zone a little above the forest floor. As has already been remarked (Haddow, 1954), if a bait lies flat down on the ground, the *Eretmapodites* tend to circle above him without biting. If he is raised slightly, as on a fallen log, they will bite.

In the *E. chrysogaster* group—as in all other *Eretmapodites* here discussed—the easily visible standing bait attracts more females than does a bait lying down. Further, a slightly moving bait is more attractive than one which is motionless. The attraction, as noted above, appears to be mainly visual.

Eretmapodites oedipodius subsp. **parvipluma.**

This species is very common around Entebbe, but unfortunately it is scarce in Bwamba (where 24-hour catching yielded only one specimen) so a comparison between the two areas is not possible.

The biting-cycle at Entebbe (Table II & fig. 2) is strikingly similar to that of the *E. chrysogaster* group in the same area. Thus the cycle is diurnal, with a slight lull in the heat of the early afternoon and a pronounced wave of activity

TABLE III.

The biting-cycles of *Eretmapodites* spp. at Entebbe and in Bwamba. The days are arranged in groups according to the time at which biting began. The days on which no biting took place until after dark have been omitted.

Species or group	Biting began at	Hour											
		06–07	07–08	08–09	09–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18
***E. chrysogaster* gp. (Entebbe)**	06–07	19	5	5	23	20	6	5	9	14	21	49	57
	07–08	0	12	5	4	5	9	1	2	3	4	20	35
	08–09	0	0	7	1	0	0	0	1	0	2	20	28
	09–10	0	0	0	3	0	0	2	0	3	1	1	5
	10–11	0	0	0	0	2	0	0	0	1	0	2	1
	11–12	0	0	0	0	0	3	1	3	4	1	2	5
	12–13	0	0	0	0	0	0	3	0	0	0	0	5
	13–14	0	0	0	0	0	0	0	0	0	0	0	0
	14–15	0	0	0	0	0	0	0	0	0	0	0	0
	15–16	0	0	0	0	0	0	0	0	0	0	0	0
	16–17	0	0	0	0	0	0	0	0	0	0	2	3
	17–18	0	0	0	0	0	0	0	0	0	0	0	3
***E. chrysogaster* gp. (Bwamba)**	06–07	25	8	6	10	16	7	2	6	12	4	6	17
	07–08	0	17	2	3	7	3	4	7	3	4	2	2
	08–09	0	0	13	1	5	3	0	1	3	1	1	3
	09–10	0	0	0	10	2	2	0	0	0	0	1	0
	10–11	0	0	0	0	6	0	3	1	1	2	0	5
	11–12	0	0	0	0	0	8	1	2	4	1	2	1
	12–13	0	0	0	0	0	0	8	1	1	1	0	1
	13–14	0	0	0	0	0	0	0	2	1	1	0	1
	14–15	0	0	0	0	0	0	0	0	10	2	0	1
	15–16	0	0	0	0	0	0	0	0	0	13	1	1
	16–17	0	0	0	0	0	0	0	0	0	0	11	1
	17–18	0	0	0	0	0	0	0	0	0	0	0	5
***E. oedipodius* subsp. *parvipluma* (Entebbe)**	06–07	12	5	6	6	1	4	1	3	7	12	24	22
	07–08	0	2	0	0	1	2	1	1	0	1	1	0
	08–09	0	0	5	1	0	0	0	0	0	1	0	9
	09–10	0	0	0	9	2	0	0	1	1	3	7	9
	10–11	0	0	0	0	5	1	0	0	1	2	2	6
	11–12	0	0	0	0	0	2	0	2	1	0	2	1
	12–13	0	0	0	0	0	0	1	0	0	2	3	2
	13–14	0	0	0	0	0	0	0	2	1	0	0	0
	14–15	0	0	0	0	0	0	0	0	0	0	0	0
	15–16	0	0	0	0	0	0	0	0	0	2	3	2
	16–17	0	0	0	0	0	0	0	0	0	0	5	6
	17–18	0	0	0	0	0	0	0	0	0	0	0	0
***E. ferox* (Bwamba)**	06–07	4	2	1	1	2	2	0	0	0	0	0	0
	07–08	0	6	1	1	0	0	0	0	0	0	0	0
	08–09	0	0	2	0	1	0	0	0	0	0	0	0
	09–10	0	0	0	3	0	1	0	0	0	0	1	0
	10–11	0	0	0	0	2	0	1	0	0	0	0	0
	11–12	0	0	0	0	0	5	3	1	2	2	1	0
	12–13	0	0	0	0	0	0	3	0	2	0	0	0
	13–14	0	0	0	0	0	0	0	6	0	1	1	0
	14–15	0	0	0	0	0	0	0	0	4	0	0	0
	15–16	0	0	0	0	0	0	0	0	0	4	0	0
	16–17	0	0	0	0	0	0	0	0	0	0	5	0
	17–18	0	0	0	0	0	0	0	0	0	0	0	5
All species collectively (Entebbe)	06–07	31	10	11	29	21	10	6	12	21	33	73	79
	07–08	0	14	5	4	6	11	2	3	3	5	21	35
	08–09	0	0	12	2	0	0	0	1	0	3	20	37
	09–10	0	0	0	12	2	0	2	1	4	4	8	14
	10–11	0	0	0	0	7	1	0	0	2	2	4	7
	11–12	0	0	0	0	0	5	1	5	5	1	4	6
	12–13	0	0	0	0	0	0	4	0	0	2	3	7
	13–14	0	0	0	0	0	0	0	2	1	0	0	0
	14–15	0	0	0	0	0	0	0	0	0	0	0	0
	15–16	0	0	0	0	0	0	0	0	0	2	3	2
	16–17	0	0	0	0	0	0	0	0	0	0	7	9
	17–18	0	0	0	0	0	0	0	0	0	0	0	3
All species collectively (Bwamba)	06–07	31	11	8	11	19	9	2	6	12	4	6	19
	07–08	0	29	3	5	9	3	4	8	3	5	3	2
	08–09	0	0	19	2	7	4	0	1	3	1	1	4
	09–10	0	0	0	16	2	3	0	0	0	0	2	0
	10–11	0	0	0	0	8	0	4	1	1	2	0	5
	11–12	0	0	0	0	0	15	4	3	6	3	3	1
	12–13	0	0	0	0	0	0	13	1	3	1	0	1
	13–14	0	0	0	0	0	0	0	8	1	2	1	1
	14–15	0	0	0	0	0	0	0	0	14	2	0	1
	15–16	0	0	0	0	0	0	0	0	0	17	1	1
	16–17	0	0	0	0	0	0	0	0	0	0	19	1
	17–18	0	0	0	0	0	0	0	0	0	0	0	13

before sunset. This wave is of longer duration than that in the *E. chrysogaster* group as it extends over three hours instead of two.

E. oedipodius is very markedly diurnal and, while nine specimens were taken in the hour after sunset (probably mainly under twilight conditions), only two were obtained during the night proper. Further, in all the catches here discussed, only one specimen was taken outside forest, and only one above ground level.

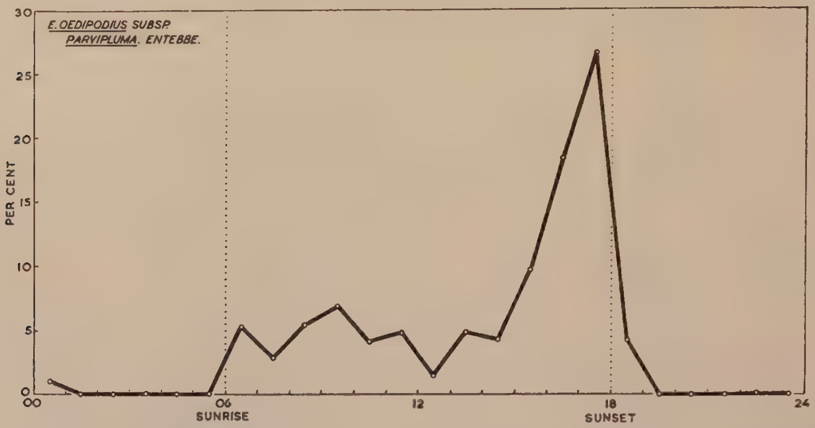


Fig. 2.—The biting-cycle of *E. oedipodius* subsp. *parvipluma*. The figures are geometric means. They have been reduced to a percentage basis to facilitate comparison with the other graphs.

While the biting-behaviour of *E. oedipodius* so closely resembles that of the *E. chrysogaster* group in the Entebbe area, it is to be emphasised that taxonomically they lie about as far apart as is possible within the limits of this very uniform and compact genus.

When the diurnal figures are analysed further by dividing the days into groups according to the time at which biting began (Table III), it will be seen that here, as in the *E. chrysogaster* group at Entebbe, biting tends to be very active just before sunset no matter at what time activity first begins. It is true that here the tendency is not so clearly marked—in some groups the biting in the first hour is roughly of the same level as that in the last hour before sunset, and in others where the numbers are small no distinct trend is obvious. If, however, the figures are combined in two-hour groups (as can easily be done mentally from the data in Table III) then it will at once be seen that in almost all groups the two-hour period before sunset shows by far the highest figures. Thus, if the crude figures in Table III are examined, it will be found that 49 per cent. of the total diurnal yield were taken in this two-hour period.

Eretmapodites ferox.

This species has so far been recorded only from the type locality, Bwamba County in western Uganda, but probably it extends far into the main lowland rain-forest of the Belgian Congo. Though very common in Bwamba, it was never taken in large numbers in 24-hour catches, as it has a distinct preference for moving baits. The biting-behaviour (Table II & fig. 3) shows a close resemblance to that of the *E. chrysogaster* group in Bwamba. Thus the cycle is diurnal, and without any very pronounced waves of activity.

When the diurnal sample is subdivided into groups of days according to the times at which biting began, as in the *E. chrysogaster* group (Table III), then it is at once apparent, in spite of the small numbers, that the tendency is for the most active biting to occur in the first hour of activity, no matter when this may be. Of the specimens listed in Table III, 64 per cent. were taken in the first hour of biting-activity. Another very noticeable feature is that the cycles tend to be very short, often only one or two hours in any given group of days. It may be noted that, as in the *E. chrysogaster* group, there were occasional days on which no biting occurred till after dark, though in such cases the numbers taken were invariably very small.

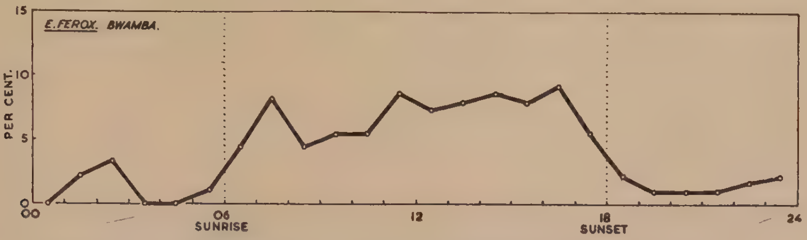


Fig. 3.—The biting-cycle of *E. ferox*. The figures are geometric means. They have been reduced to a percentage basis to facilitate comparison with the other graphs.

Thus the biting-behaviour of *E. ferox* in Bwamba closely resembles that of the *E. chrysogaster* group in the same area. It should be stressed that taxonomically *E. ferox* is not closely related to *E. chrysogaster*.

The **Eretmapodites inornatus** group.

No members of this group were taken in the Entebbe area. In Bwamba it consists almost entirely of two species, *E. inornatus* and *E. penicillatus*. As in the case of the *E. chrysogaster* group, females of the *E. inornatus* group cannot be distinguished in life. *E. tonsus*, which lies between this group and *E. quinquevittatus*, does occur, but is exceedingly rare. So also, for that matter is *E. quinquevittatus*.

Mosquitos of the *E. inornatus* group are never common and the present sample (58 specimens) is rather small for discussion. The results in Table II would seem to indicate that a larger proportion of females in this group bite by night than is the case with the other species here discussed, but actually this is almost entirely due to a single exceptional catch and in the main the cycle is diurnal. This has been confirmed by the results of mass catches made by day and by night, which provide a much larger sample.

The numbers seem too small to warrant the inclusion of a Table further subdivided according to the times at which biting began. It may be mentioned, however, that such a Table has been worked out and that it shows the usual Bwamba tendency for the most active biting to occur in the first hour, no matter when that may be. Thirty five mosquitos of this group were taken biting by day and of these 20 (or 57%) were taken in the first hour of biting-activity.

Eretmapodites leucopus subsp. **productus.**

The specimens taken in 24-hour catches are too few to permit discussion. Routine mass catches, however, have shown that this species is essentially diurnal.

Discussion.

The main point emerging from the above is that, while the species studied are essentially diurnal, the behaviour in different areas is quite dissimilar. In

Bwamba County, these mosquitos tend to be very active during the first hour of biting-activity, while in Entebbe the main wave comes just before sunset, no matter at what time biting has begun. Thus summation of results for the various Bwamba species produces in each case a series of curves, essentially diurnal, but without any very striking characteristics, while similar summation for Entebbe gives curves characterised by a very marked wave of activity just before sunset. The results for the two areas seem sufficiently consistent to justify the preparation of a general curve for each area, showing all species collectively (Tables II & III & fig. 4) and including all the 568 Bwamba and 695 Entebbe specimens. Thus general Bwamba-type and Entebbe-type cycles are obtained, quite divergent in form owing to fundamental differences in behaviour. Thus from the general figures in Table III the following interesting percentages may be computed:—

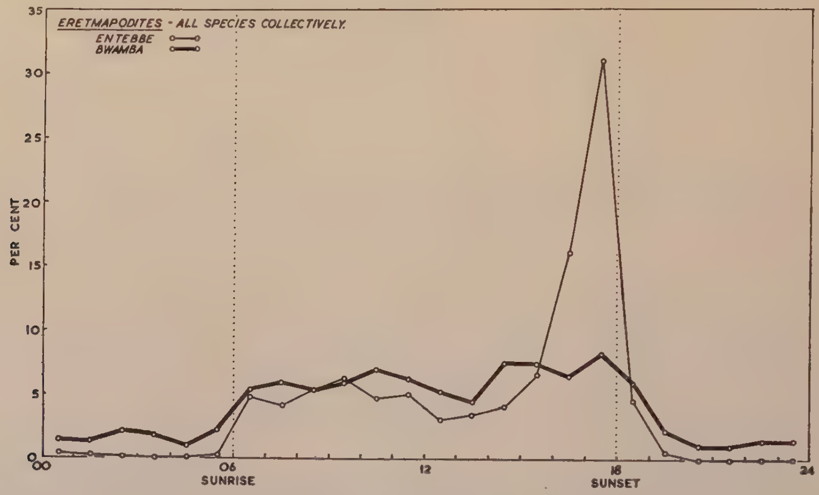


Fig. 4.—The collective biting-cycles for the two areas. The figures are geometric means. They have been reduced to a percentage basis to facilitate comparison with the other graphs.

Locality	Percentage of the total diurnal yield taken in the first hour of biting	Percentage of the total diurnal yield taken in the hour before sunset
Entebbe	15	30
Bwamba	47	11

The Entebbe figures become still more striking if the two hours before sunset are considered together, as in this period 52 per cent. of the total diurnal yield was taken.

As the *E. chrysogaster* group behaves quite differently in Bwamba and at Entebbe, and as its behaviour in one area is paralleled by that of a quite dissimilar species (*E. oedipodius*) and in the other by equally dissimilar species (*E. ferox* and the *E. inornatus* group) it seems likely that an environmental influence of some sort may be responsible. What this influence may be, however, is a question which cannot at the moment be answered.

In a recent paper (Haddow, 1954) the writer advanced the view that while in the past it had been considered that the behaviour of mosquitos in the field was actively conditioned by microclimate, this standpoint was now difficult to maintain. It was suggested that the response to microclimate could with better reason be regarded as having a basis of inhibition. Thus, mosquitos should be considered as being inhibited from biting by unfavourable microclimate and that with the return of favourable conditions they were merely, as it were, released. Whether or not they then began to bite must depend, it was suggested, on some other factor connected, perhaps, with age or physiological state. While this view has proved a helpful one in the case of certain groups, it fails to explain the present situation, as does also the age-group theory advanced by Lumsden (1952).

While there are considerable differences between the forest environments of Bwamba and Entebbe, it is not felt that these are of an order which is likely to explain the differences noted, and this applies also in the case of weather and microclimate. For the time being, therefore, there is no alternative but to record the differences observed without further attempt at explanation.

Summary.

The biting-habits of mosquitos in the genus *Eretmapodites* Theobald, as shown by 24-hour catches, display a certain uniformity in that all the species studied are essentially diurnal and bite very close to the ground, in shade. They do not enter dwellings.

When, however, two localities are compared (the Entebbe area and Bwamba County) it is found that there is a fundamental difference in behaviour. At Entebbe there is an exceedingly well-marked wave of activity before sunset. This does not occur in Bwamba, where the cycle shows no pronounced characteristics apart from its generally diurnal nature. It is shown that this difference arises from the fact that in Bwamba the first hour of biting-activity tends to be the most intense (no matter when it occurs) whereas in Entebbe the hour before sunset is almost always preferred.

One group (the *E. chrysogaster* group) is present in both localities. In Entebbe it shows an activity curve of the one type, and in Bwamba a curve of the other type.

It is concluded that some environmental influence must be involved. At the moment, however, no suggestion can be made concerning the nature of this influence, beyond the fact that the activity-patterns concerned are not easily explained in terms of microclimate.

References.

Bauer, J. H. (1928). The transmission of yellow fever by mosquitoes other than *Aëdes aegypti*.—Amer. J. trop. Med., **8**, pp. 261–282.

Edwards, F. W. (1941). Mosquitoes of the Ethiopian region. III. Culicine adults and pupae.—499 pp. London, Brit. Mus. (Nat.Hist.).

Garnham, P. C. C., Harper, J. O. & Highton, R. B. (1946). The mosquitos of the Kaimosi Forest, Kenya Colony, with special reference to yellow fever.—Bull. ent. Res., **36**, pp. 473–496.

Haddow, A. J. (1945*a*). On the mosquitoes of Bwamba County, Uganda. I. Description of Bwamba, with special reference to mosquito ecology. —Proc. zool. Soc. Lond., **115**, pp. 1–13.

Haddow, A. J. (1945*b*). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.— Bull. ent. Res., **36**, pp. 33–73.

Haddow, A. J. (1945*c*). The mosquitoes of Bwamba County, Uganda. III. The vertical distribution of mosquitoes in a banana plantation and the biting cycle of *Aëdes* (*Stegomyia*) *simpsoni* Theo.—Bull. ent. Res., **36**, pp. 297–304.

Haddow, A. J. (1946). The mosquitoes of Bwamba County, Uganda. IV. Studies on the genus *Eretmapodites*, Theobald.—Bull. ent. Res., **37**, pp. 57–82.

Haddow, A. J. (1954). Studies of the biting-habits of African mosquitos. An appraisal of methods employed, with special reference to the twenty-four-hour catch.—Bull. ent. Res., **45**, pp. 199–242.

Haddow, A. J., Gillett, J. D. & Highton, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate.—Bull. ent. Res., **37**, pp. 301–330.

Hoogstraal, H. & Knight, K. L. (1951). Observations on *Eretmapodites silvestris conchobius* Edwards (Culicidae) in the Anglo-Egyptian Sudan. —Amer. J. trop. Med., **31**, pp. 659–664.

Kerr, J. A. (1933). Studies on the abundance, distribution and feeding habits of some West African mosquitos.—Bull. ent. Res., **24**, pp. 493–510.

Lumsden, W. H. R. (1952). The crepuscular biting activity of insects in the forest canopy in Bwamba, Uganda. A study in relation to the sylvan epidemiology of yellow fever.—Bull. ent. Res., **42**, pp. 721–760.

Macnamara, F. N. (1953). The susceptibility of chicks to Semliki forest virus (Kumba strain).—Ann. trop. Med. Parasit., **47**, pp. 9–12.

Smithburn, K. C. & Haddow, A. J. (1944). Semliki forest virus. I. Isolation and pathogenic properties.—J. Immunol., **49**, pp. 141–157.

Smithburn, K. C., Haddow, A. J. & Gillett, J. D. (1948). Rift Valley fever. Isolation of the virus from wild mosquitoes.—Brit. J. exp. Path., **29**, pp. 107–121.

Smithburn, K. C., Haddow, A. J. & Lumsden, W. H. R. (1949). Rift Valley fever: transmission of the virus by mosquitoes.—Brit. J. exp. Path., **30**, pp. 35–47.

van Someren, E. C. C. (1947). Ethiopian Culicidae—the description of a new *Eretmapodites* Theobald.—Proc. R. ent. Soc. Lond., (B) **16**, pp. 13–15.

van Someren, E. C. C. (1949). Ethiopian Culicidae—*Eretmapodites* Theobald: description of four new species of the *chrysogaster* group with notes on the five known species of this group.—Proc. R. ent. Soc. Lond., (B) **18**, pp. 119–129.

Williams, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems.—Ann. appl. Biol., **24**, pp. 404–414.

TROGODERMA AFRUM PRIESNER, A SYNONYM OF *T. GRANARIUM* EVERTS AND A COMPARISON WITH *T. VERSICOLOR* (CREUTZ.).

By R. W. Howe and H. D. Burges

The two species of *Trogoderma* most frequently recorded from stored products in Britain, *T. granarium* Everts and *T. versicolor* (Creutz.) are both widely distributed throughout the world. There is some difficulty in distinguishing these species by the external features of the adult and it seems very likely that on occasions specimens of *T. granarium* have been erroneously named as *T. versicolor*. In addition, Prof. Priesner has recently (1951) published a description of a new species from Egypt and the Sudan, *T. afrum*, which is very similar to *T. granarium* and in previous literature had been discussed under that name. Consequently, the differences between these three species have been examined, using breeding experiments as well as morphological comparisons.

Hinton (1945) gives detailed descriptions of the species of *Trogoderma* found in stored products and summarises the published information on their distribution, habits and life-cycles. A. B. Hadaway, in an unpublished thesis (1945), gives a detailed comparison of the morphology and biology of *T. granarium* and *T. versicolor*. The biological part of this thesis is published in this issue (Hadaway, 1955).

The very full descriptions given by Hinton establish the identity of the species considered here. We understand, however, from Mr. J. Balfour-Browne of the British Museum (Natural History) that the species known by the name *T. versicolor* in eastern Europe differs from the current British conception of that species. He considers that the eastern European species is probably the true *T. versicolor* and that the species described by Hinton is the American *T. inclusum* Lec. The question cannot be settled by reference to the type of the former because that was destroyed by a bomb during the recent war.

Distribution.

T. granarium has been found in most of the hot dry areas of the world in stored cereals. It has caused serious damage in India (Barnes & Grove, 1916), Cyprus, Egypt (Zacher, 1935), Anglo-Egyptian Sudan (Darling, 1951) and Nigeria (Howe, 1952) and has recently been discovered in California (Dorward, 1953). In Britain and elsewhere in Europe it attacks dry malt stored in warm malt bins (Munro, 1940; Voelkel, 1924). *T. versicolor* is more typically a pest of produce of animal origin, but it has been recorded from stored grain in some of the areas in which *T. granarium* occurs. These include India (Arrow, 1915), Cyprus (Wilkinson, 1925), Egypt (Zacher, 1935), Britain (Munro, 1940), Europe (Zacher, 1927) and California (Linsley & Michelbacher, 1943).

The Problem of naming Specimens.

These two species are not as easily separated as might be anticipated although typical specimens examined side by side are clearly different. There are a number of features which might cause a collector to give a specimen of *T. granarium* the name *T. versicolor*. Hinton suggests that Wilkinson may have done so, and certainly *T. granarium* appears to be commoner than *T. versicolor* in Cyprus. The chief cause of confusion is the elytral pattern which is superficially similar in living specimens of the two species, but often fades or disappears in dried specimens of *T. granarium*. Thus Priesner (1951) states that *T. granarium* "has no distinct pale markings on the elytra, and no defined patches of hairs on them." There is therefore a tendency to call a *T. granarium* with a distinct pattern by some other name. Unfortunately, the black ground colour of *T. versicolor* is not entirely constant, and although *T. versicolor* is on average larger than *T. granarium*, the overlap of size is sufficient to render this character more or less useless. Hinton considers that the emarginate eye of *T. versicolor* is sufficient to differentiate it from all the other storage species of *Trogoderma*, but although this is true, it is not an easy character to appreciate because the limits of the eye are difficult to define on a dark head and also because there often appears to be a slight emargination in the eye of *T. granarium*.

The antennal characters are adequate to distinguish the species but must be used with care. Hadaway gives some additional characters which enable the species to be separated with certainty. Hinton regards as diagnostic the fringe of suberect hairs parallel to the apical margin of the fifth abdominal segment of the male *T. granarium*.

Willcocks (1925) recorded only *T. versicolor* from Egypt but Zacher (1935) recorded *T. granarium* as well. Priesner (1951) appears to have decided that there is only one species in Egypt. He examined it very carefully and described it as a new species, *T. afrum*, similar in many ways to *T. granarium*, but differing from it in the antennae. The elytra of *T. afrum* also bore dark and pale markings in which he believed it to differ from *T. granarium*. This erroneous belief, and the difficulty of making reliable identifications by use of the antennal characters alone, suggested the possibility that Prof. Priesner's new species might be a maculate form of *T. granarium*. This opinion was supported by the knowledge that many specimens from Egypt and the Sudan as well as from Iraq, Cyprus and N. Africa had been identified in Britain as *T. granarium* or *T. versicolor*.

Dr. Abd el Hakim Kamel of the Egyptian Ministry of Agriculture very kindly sent us living specimens of the common Egyptian *Trogoderma*, and Dr. S. Mukerji of the Indian Agricultural Research Institute sent dead adults of the native Indian *T. granarium*. These specimens were compared with culture material of *T. granarium* and *T. versicolor* bred at this laboratory for many years and with *T. granarium* collected recently from British maltings and from groundnuts in Nigeria. Also, pupae of the Egyptian *T. afrum*, of *T. versicolor* from cultures, and of *T. granarium* from cultures and from maltings were isolated and sexed. The emerging adults were set up in pairs, a male of one species being placed with a female of another in a glass tube with a little wheat and middlings. About fifteen pairs of each of the three crosses were set up.

The Identity of *T. afrum*.

There are two larval and several adult characters which can be used to separate *T. granarium* from *T. versicolor*. Examination of adults of *T. afrum* showed that it was identical with all the groups of *T. granarium* in all but one of these characters. This character is the antenna in which there are slight differences between the species. The figures given by Hinton and Priesner differ markedly, but this may be caused by a difference in the position of the antennae when drawn. The differences in the specimens examined by us did not permit confident separation of the beetles into named groups. On morphological grounds, therefore, without having examined type specimens, we conclude that *T. afrum* is almost certainly a synonym of *T. granarium*.

Not one of the attempts to cross *T. versicolor* with *T. granarium* or *T. afrum* was successful, but 17 of the 19 matings of *T. granarium* and *T. afrum* produced fertile cultures. This supports the suggestion that these are a single species. There does remain, of course, the slight possibility that the specimens we received from Egypt were not the same species as that described by Priesner. This can only be resolved by a dissection of the two type specimens of the species.

Comparison of *T. granarium* and *T. versicolor.*

The larvae of *Trogoderma* are clothed with simple and barbed hairs. In the barbed hairs the shaft is constricted at regular intervals. It ends in a barbed head equal in length to three or four of the preceding segments. Barbed hairs are arranged into definite tufts on the postero-lateral margins of abdominal tergites 5 to 8 in fully grown larvae. In the first-instar larvae, however, the tufts are restricted to segments 7 and 8. In *T. granarium* each tuft consists of only four to ten barbed hairs but in *T. versicolor* there are 18–24 hairs in each tuft.

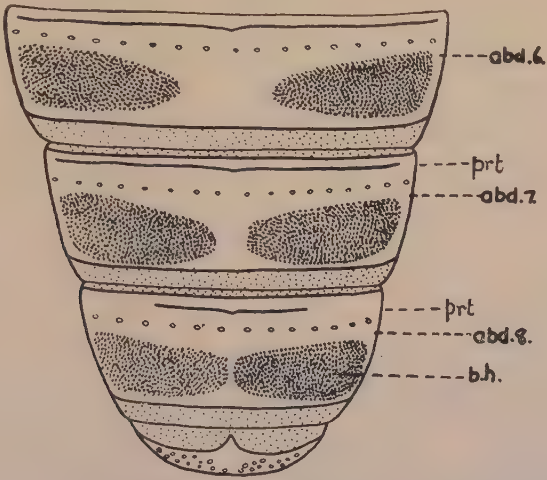


Fig. 1.—*T. versicolor.* Dorsal view of sixth to ninth abdominal segments of larva: *abd.6*, 6th abdominal segment; *b.h.*, bases of barbed hairs; *prt*, pretergal line.

With each moult, the number of hairs in a tuft increases and so this character is not diagnostic for older larvae. These can be distinguished by the presence or absence on segments 7 and 8 of the pretergal line which runs parallel and close to the anterior margin of the abdominal tergites. It is present on both segments in *T. versicolor* (fig. 1) but in *T. granarium* it is absent from tergite 8 and either faint or absent from tergite 7.

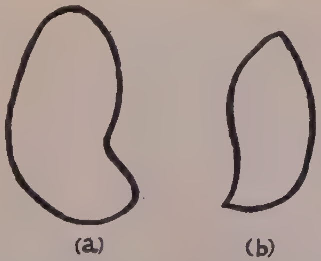


Fig. 2.—Dorsal view of right eye of *T. versicolor* (a); left eye of *T. granarium* (b).

The adult of *T. versicolor* is in general larger than that of *T. granarium* but not only does size vary widely with the quality of food, environmental conditions and crowding, but there is also a sex difference of size in both species. The female is larger than the male, an average-sized male of *T. versicolor* being about the same size as a typical female *T. granarium*.

The compound eye of *T. versicolor* (fig. 2, a) has a definite emargination on its inner margin but that of *T. granarium* (fig. 2, b) is more regular in outline. The antennal club differs between the species in both sexes. In the male *T. versicolor* the club is composed of 6–7 segments, in the male *T. granarium* of 5 segments, in the female *T. versicolor* of 4–5 segments and in the female *T. granarium* of 4 segments.

The ground colour of the elytra of *T. versicolor* is black with pale brown transverse bands, whereas the ground colour of *T. granarium* is reddish brown with the transverse marks vague but dark.

The males can be distinguished by one other external character. In *T. granarium* there is a dense fringe of moderately stout suberect hairs near and more or less parallel to the apical margin of the fifth abdominal sternite. This is not found in *T. versicolor*.

When the Commonwealth Institute of Entomology identified Nigerian specimens of *T. granarium* in 1949, they compared them with specimens of *T. versicolor*. They reported that the wings of *T. granarium* were reduced in size to about the length of the elytra while those of *T. versicolor* were larger. In our

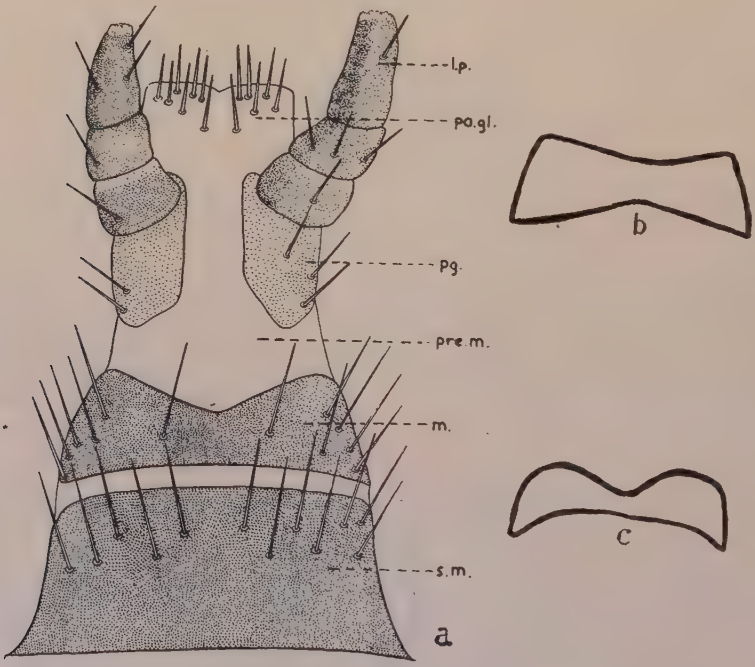


Fig. 3.—(a) labium of adult *T. versicolor*, ventral view; (b) mentum of *T. versicolor*; (c) mentum of *T. granarium*. *l.p.*, labial palp; *pa.gl.*, paraglossa; *pg.*, palpiger; *pre.m.*, prementum; *m.*, mentum; *s.m.*, submentum.

culture specimens of *T. versicolor*, the wing is also reduced and is very similar to the wing of *T. granarium*.

The remaining differences, which require dissection of the mouth-parts and genitalia, are clear-cut. In the mouth-parts the anterior margin of the mentum is deeply emarginate in *T. granarium* (fig. 3, c), and much less emarginate in *T. versicolor* (fig. 3, a, b). The mentum sclerite is reduced in depth at the middle to less than half its depth at the margin in *T. granarium*, but only to two-thirds in *T. versicolor*. Each side of the anterior margin is rounded in *T. granarium* and straighter in *T. versicolor*.

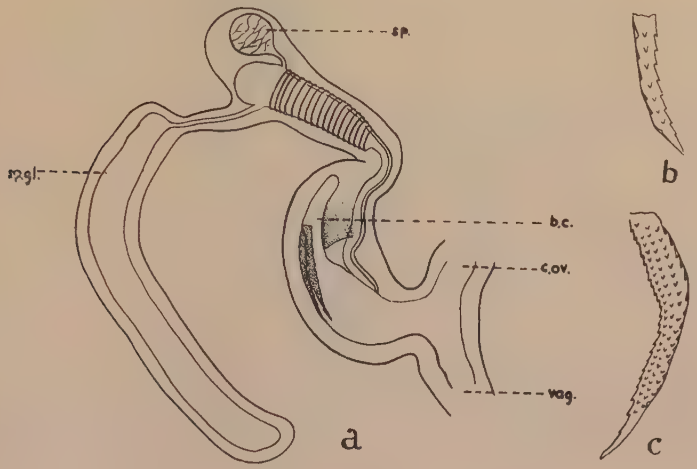


Fig. 4.—(a) bursa copulatrix and spermatheca of *T. granarium*; (b) paired sclerite of *T. granarium*; (c) paired sclerite of *T. versicolor*. *b.c.*, bursa copulatrix; *c.ov.*, common oviduct; *sp.*, spermatheca; *sp.gl.*, spermathecal gland; *vag.*, vagina.

In the female genitalia, the paired sclerites of the bursa copulatrix (fig. 4, a) bear few teeth in *T. granarium* (fig. 4, b) but many in *T. versicolor* (fig. 4, c). The

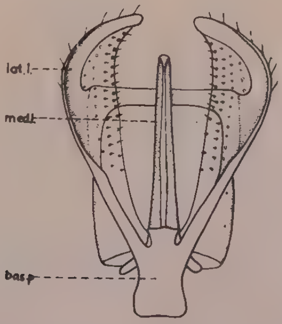


Fig. 5.—Dorsal view of aedeagus of male *T. granarium*. *bas.p.*, basal piece; *med.l.*, median lobe; *lat.l.*, lateral lobe.

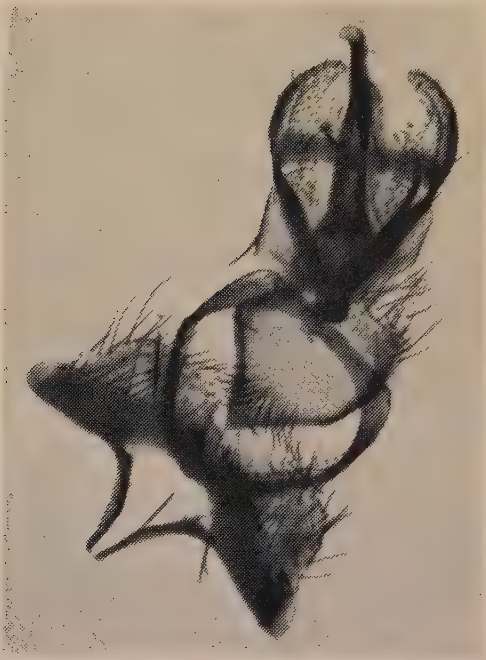


Fig. 6.—Photograph of male genitalia of *T. granarium* showing relative positions of aedeagus and ring segment.

male genitalia (figs. 5 & 6) are closely similar but the ninth abdominal or ring segment is rounded ventrally in *T. granarium* (fig. 7, a) but is flattened in *T. versicolor* (fig. 7, b).

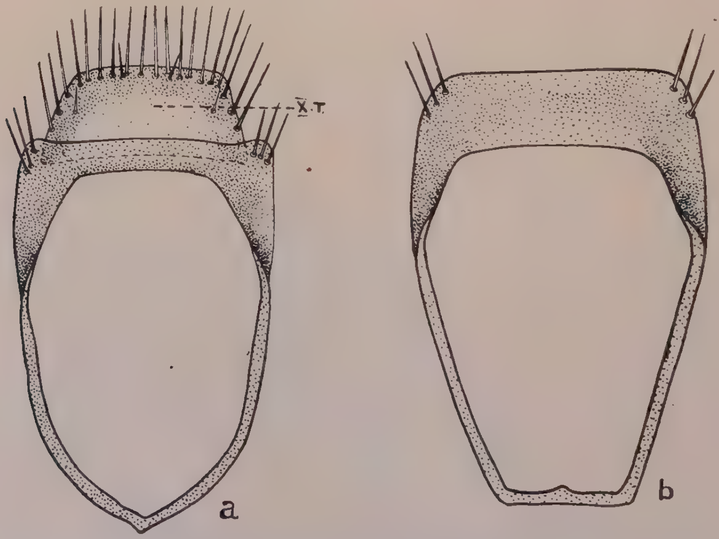


Fig. 7.—Ninth and tenth abdominal tergites of male of *T. granarium* (a) and *T. versicolor* (b). *X.T.*, 10th tergite.

Summary.

The common Egyptian *Trogoderma*, *T. afrum* Priesner, is compared morphologically with the widespread *T. granarium* Everts and found to be almost identical. The two interbreed and are therefore considered to be conspecific. The morphological differences between *T. granarium* and *T. versicolor* (Creutz.) are described. These species do not interbreed.

Acknowledgements.

We must extend grateful thanks to Dr. A. B. Hadaway and to the University of London for permission to quote from the thesis "The biology of the beetles *Trogoderma granarium* Everts and *Trogoderma versicolor* Creutzer" which was submitted for the degree of Ph.D. in 1945. All our figures except numbers 2, 3, b, 3, c and 6 were taken from this thesis. We must also record our appreciation of the help given by Dr. Abd el Hakim Kamel and Dr. S. Mukerji in sending us specimens of *Trogoderma* from Egypt and India. Thanks are also due to the Commonwealth Institute of Entomology for confirming the identity of *T. granarium* collected in Nigeria and Cyprus.

This work forms part of the programme of the Pest Infestation Laboratory and is published with the permission of the Department of Scientific and Industrial Research.

References.

ARROW, G. J. (1915). Notes on the Coleopterous family Dermestidae, and descriptions of some new forms in the British Museum.—Ann. Mag. nat. Hist., (8) **15**, pp. 425–451.

BARNES, J. H. & GROVE, A. J. (1916). The insects attacking stored wheat in the Punjab and the methods of combating them, including a chapter on the chemistry of respiration.—Mem. Dep. Agric. India, Chem. Ser., **4**, pp. 165–280.

DARLING, H. S. (1951). Insects and grain storage in the Sudan.—Sudan Notes, **32**, pp. 131–149.

DORWARD, K. (1953). The U.S. insect situation at year's end.—Agric. Chem., **8**, no. 12, pp. 61–62.

HADAWAY, A. B. (1955). The biology of the Dermestid beetles, *Trogoderma granarium* Everts and *Trogoderma versicolor* (Creutz.).—Bull. ent. Res., **46**, pp. 781–796.

HINTON, H. E. (1945). A monograph of the beetles associated with stored products. Volume 1.—443 pp. London, Brit. Mus. (Nat. Hist.).

HOWE, R. W. (1952). Entomological problems of food storage in northern Nigeria.—Bull. ent. Res., **43**, pp. 111–144.

LINSLEY, E. G. & MICHELBACHER, A. E. (1943). A report on insect infestation of stored grain in California.—J. econ. Ent., **36**, pp. 829–831.

MUNRO, J. W. (1940). Report on a survey of the infestation of grain by insects.—54 pp. London, Dep. sci. industr. Res.

PRIESNER, H. (1951). Description of the common Egyptian *Trogoderma* (Coleoptera: Dermestidae).—Bull. Soc. Fouad 1er Ent., **35**, pp. 133–135. 41

VOELKEL, H. (1924). Zur Biologie und Bekämpfung des Khaprakäfers, *Trogoderma granarium* Everts.—Arb. biol. Reichsanst., **13**, pp. 129–171.

WILKINSON, D. S. (1925). Entomological notes.—Cyprus agric. J., **20**, pp. 9–10.

WILLCOCKS, F. C. (1925). The insect and related pests of Egypt. Vol. II. Insects and mites feeding on gramineous crops and products in the field, granary and mill.—418 pp. Cairo, Sultanic agric. Soc.

ZACHER, F. (1927). Die Vorrats-, Speicher- und Materialschädlinge und ihre Bekämpfung.—366 pp. Berlin, Parey.

ZACHER, F. (1935). Die Vorratsschädlinge Ägyptens.—Mitt. Ges. Vorratsschutz, **11**, pp. 42–44, 78–82.

THE BIOLOGY OF THE DERMESTID BEETLES, *TROGODERMA GRANARIUM* EVERTS AND *TROGODERMA VERSICOLOR* (CREUTZ.).*

By A. B. Hadaway
Colonial Insecticides Research Unit, Porton.

Lepesme (1938) gave a short review of the economically important members of the 85 world species of the Dermestid beetles of the genus *Trogoderma.* Three species of this genus occur in Britain. A survey of granaries, maltings and warehouses throughout this country has shown that only two of these are of economic importance; they are *Trogoderma granarium* Everts and *Trogoderma versicolor* (Creutz.). The former is a more common pest, but both do much damage to stored products, particularly stored malt and grain. The third species, *Trogoderma megatomoides* Rter., has been recorded in England by Richards (1941) in collections of dried insects.

T. versicolor was recorded in 1904 by Ganglbauer on flowers, in old wood, and attacking insect collections. The Gipsy Moth (*Lymantria dispar* (L.)) is a pest of cork oak in Morocco, and in 1930 de Lépiney mentioned *T. versicolor* as one of the beetles destroying the egg-masses of this moth. In America, Pettit (1930) found it destroying dried sweet maize kept for seed and, in Canada, Twinn (1932) recorded it as a pest of woollen cloth, cereals, and dried-milk products. Solodovnikova (1937) reported infestations in flour mills and storehouses in Russia. Recently, it has been found in Britain on stored malt, wheat, barley and dried-milk products, as well as on dried insect collections.

T. granarium is a native of India, where it is one of the most important enemies of grain. Cotes (1893 & 1894) and Lefroy (1906) recorded it there, and later, in 1916, Barnes & Grove gave an account of its life-history. The vernacular name of "Khapra" beetle was given to it. This species was introduced into this country comparatively recently. It was recorded by Walker (1917) as found in 1908 in screenings of Karachi barley at a granary in Strood, Kent. In 1917, Arrow described a species new to Britain under the name of *Trogoderma khapra,* which subsequently was shown to be *T. granarium.*

A recent survey in this country shows that the Khapra Beetle is confined to vegetable products and that it occurs on malt, and to a lesser extent on wheat, barley, kibbled rice, rice, flour, peas, beans, groundnut curves and groundnut cake. In Germany too, it has been introduced only recently and has become a pest in malthouses (Voelkel, 1924). In Japan, however, Nakayama (1931) described it as an important pest of stored rice.

In England, these two species are serious pests only in maltings. Malt is often stored, for as long as a year before it is used for brewing, in large deep wooden bins situated close to the kiln shafts to exclude moisture. Measurements taken in bins showed temperatures of 24°–26°C. and relative humidities of 25–35 per cent. In modern maltings, storage is often at air temperature in steel- or concrete-lined bins. The effects of environmental conditions upon the duration of the different stages in the life-cycle of *T. granarium* and *T. versicolor* are given, together with an account of the life-history, in this paper.

---

* This work was carried out in 1938–40 under the direction of Professor J. W. Munro while the author was a Ph.D. student at the Imperial College of Science Biological Field Station at Slough.

Life-histories of *T. granarium* **and** *T. versicolor.*

Eggs.

The eggs of the two species are deposited singly and are not cemented by secretions to a substratum. Some eggs are deposited loosely among the grain; the others are placed in grooves or cracks formed by the removal of the dried shoots at the ends of the grains. The female makes use of the existing crevices and does not penetrate the husk or damage the grain in any way.

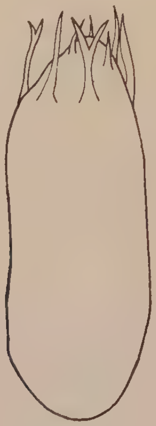


Fig. 1.—Egg of *T. granarium* (× 75).

A typical egg (fig. 1) is cylindrical, average measurements being 0·7 mm. long and 0·25 mm. broad. One end is rounded; the other is more pointed and bears a number of spine-like projections broader at the base and tapering distally. When first deposited, the egg is milky white in colour, but as development proceeds it takes on a pale yellowish colour. As the time for hatching approaches, the brown tergites and hairs of the developing larva become visible dorsally through the transparent egg membrane. Anteriorly, the two groups of ocelli are visible as dark spots. The rounded end of the egg becomes dark brown owing to the presence of hairs on the posterior part of the larva, and the long " tail " which is coiled between the larva and the posterior end of the egg case.

Emergence of the first-stage larva occurs at the end of the egg bearing spine-like projections. The larva breaks through the egg membrane, crawls free head first and leaves behind a shiny transparent egg case. Sometimes, especially at low temperatures, the larva remains for some time with the " tail " still within the egg case.

Larvae.

The first-stage larva (fig. 2) has a total length of 1·6 to 1·8 mm., a little more than half of which consists of a long " tail ", made up of a number of hairs borne on the last abdominal segment. The body width is 0·25 to 0·3 mm. It is uniform yellowish white in colour, except for the head and body hairs which are brown.

The head is prognathous with biting mouth parts, the mandibles being conspicuous by their dark colour. The head bears a short three-jointed antenna and six ocelli on each side. The prothorax is longer than each of the remaining body segments. Each thoracic segment bears a pair of legs of the Polyphaga type, with a tibiotarsus and single claw. Eight abdominal segments are clearly visible, and a small ninth segment is also present.

A characteristic feature of the larva is the presence of two kinds of body hairs, illustrated in fig. 3.

1. "Simple" hairs, in which the shaft bears many small, stiff, upwardly directed processes.
2. "Barbed" hairs, in which the shaft is constricted at regular intervals, and in which the apex consists of a barbed head. The head is as long as the combined lengths of four of the preceding segments.

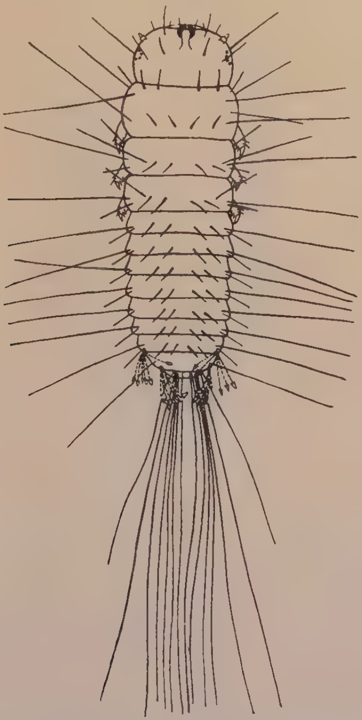


Fig. 2.—First-stage larva of *T. granarium* (× 50).

Simple hairs are scattered over the dorsal surface of the head and body segments. Those projecting laterally are as long as the body is broad. The tail consists of two groups of long simple hairs, borne on the ninth abdominal segment. Barbed hairs are found on the first-stage larva in two pairs of tufts, borne on the postero-lateral margins of the seventh and eighth abdominal tergites. On the first-stage larva of *T. granarium* there are 4 to 10 barbed hairs per tuft, and on that of *T. versicolor* there are usually 18 to 24 per tuft.

At each moult, the old larval skin splits along the mid-dorsal line from the posterior margin of the head to the fifth or sixth abdominal segment. The larva crawls out, leaving the cast skin behind, and begins to feed again immediately. The cast skins can be seen on cultures of heavily infested grain.

The number of instars varies, and no definite number can be given for any given conditions of temperature and humidity. In fact, the number varies even among the individuals from the same batch of eggs from one female and kept under the same conditions. The female usually undergoes one more moult than the male. Twenty five larvae of *T. granarium* were kept in individual tubes at 35°C. and a relative humidity of 50 per cent., and the numbers of moults were as follows:—

	4 moults	5 moults
Male	7	3
Female	0	15

At lower temperatures, the number of moults varies more and is often between five and eight. The period between moults at 35°C. is four or five days, but at lower temperatures becomes very much lengthened, the larva passing into a state of quiescence.

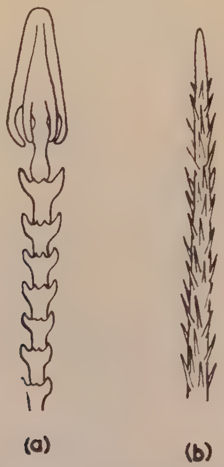


Fig. 3.—Ends of (a) barbed and (b) simple hairs.

As development proceeds and the larva increases in size, the colour changes progressively from the pale yellowish white of the first-stage larva to a golden or reddish brown. The density of the body hairs increases, but these and the tail become much shorter in proportion to the length and breadth of the larval body.

The first larval instar of *T. granarium* has paired tufts of barbed hairs on the eighth and seventh abdominal tergites, each consisting of 4 to 10 hairs. These tufts are more dense in the second-stage larva, and a few barbed hairs are present on the sixth abdominal tergite. The third-stage larva has a few barbed hairs on the fifth tergite, together with an increase in density of the other three pairs.

These four pairs of tufts are very dense in the fourth instar, they are dark brown in colour and give the appearance of four dark transverse bands. In addition, a few barbed hairs appear on the posterior lateral areas of each thoracic and remaining abdominal tergites. The fifth and any subsequent instar resembles the fourth, except for an increase in body size and density of hairs. When reared under similar conditions the mature larva of *T. versicolor* (fig. 4) is rather larger than that of *T. granarium*, approximate measurements being: length, 7 mm. and 5 mm., breadth, 2 mm. and 1·5 mm. respectively. Morphologically the two species are very similar, but may be separated by the presence or absence of a dark pretergal line on the 7th and 8th abdominal segments. In *T. granarium* such a line is faint or absent on the 7th segment and is never present on the 8th segment.

It has been suggested that the larval hairs form a defensive weapon in that they keep such enemies as parasitic Hymenoptera, Coleoptera, and mites at a distance. Since the pupa, and the adult while it hardens, remain in the last larval skin, the hairs would be of some use during these critical periods for protection against predacious enemies. On the other hand, they definitely enable the larva to remain on rough surfaces. By this means, the larvae are able to cling to sacks, even when they are dragged from one place to another, and similarly they can be transported on the clothing of workmen. Infestations are spread from one part of a malting to another, or from an infested building to one free from insects, in this way. It is suggested that they can be spread by means of animals such as rats and mice infesting the bins.

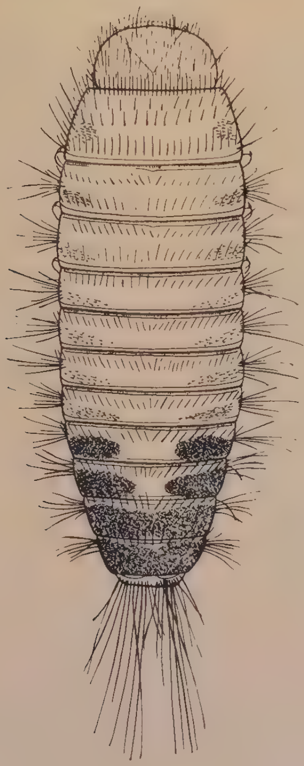


Fig. 4.—Mature larva of *T. versicolor* (× 12).

The larvae are responsible for the damage to grain. Voelkel (1924) and Barnes & Grove (1916) stated that young larvae cannot attack whole grain and are unable to penetrate such grain until after the third moult. Usually malt grains are slightly damaged at the ends where the dried shoots have been broken off. On closer examination, grain which appears to the naked eye to be whole and sound shows small lesions on the bran. The young larvae apparently can attack whole grain by biting through the bran. *Trogoderma* larvae feed on the germ and endosperm of malt grain, sometimes completely hollowing out the grain until only the husk remains. Often the only parts of wheat grain eaten are the germ and the bran which covers it, although the adjacent endosperm is sometimes eaten.

Pupae.

At the last ecdysis, the larval skin splits dorsally from the posterior margin of the head to the fifth or sixth abdominal tergite, but is not cast off, the pupa remaining within this skin for the whole of its life (fig. 5, a). The thorax and anterior part of the abdomen of the pupa are wider than the corresponding parts of the larva and the last larval skin gapes open so that a part of the dorsal surface of the pupa is seen. This is densely clothed with hairs.

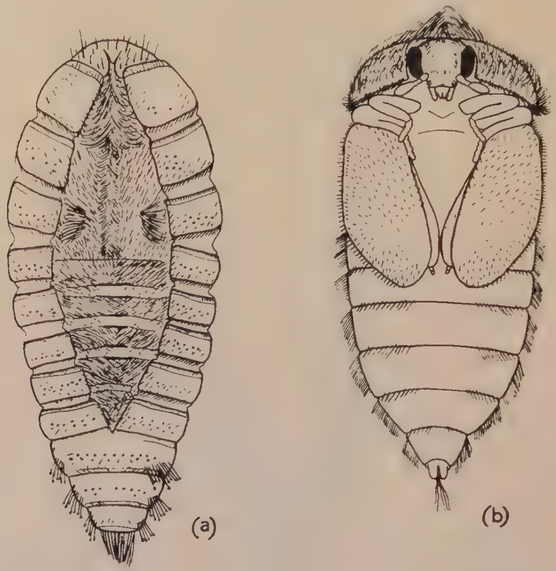


Fig. 5.—Female pupa of *T. versicolor* (× 12): (a) in last larval skin, dorsal view; (b) removed from last larval skin, ventral view.

The pupa (fig. 5, b) is of the exarate type. The male is smaller than the female, average lengths for *T. granarium* being: male 3·5 mm., female 5 mm., and for *T. versicolor*: male 4·5 mm., female 6 mm. The pupae are usually to be found near the surface of grain.

Adults.

When the adult beetle emerges, the pupal skin is cast off and remains within the posterior end of the larval skin. The adult beetle remains enclosed within the larval skin for a short time, varying from a day or more according to conditions, while the cuticle hardens and pigmentation takes place.

The sex of the adult beetles may be determined by their size and antennal characters. The male is smaller than the female, its antennal club is looser and consists of more segments, and the terminal segment of the antenna is twice as long as it is broad, whereas in the female it is no longer than it is broad.

T. granarium is a small oblong-oval beetle measuring 1·6–3·0 mm. in length and 0·9–1·7 mm. in breadth. The male is smaller than the female, average lengths being 2 mm. and 3 mm., respectively.

The head is small and usually deflexed so that in dorsal view most of it is hidden under the pronotum. The compound eyes are usually rounded. The antennae are 11-segmented. In the male, the first and second segments are large, and the third to the sixth are small. The seventh segment is enlarged so that it may be considered to belong to the antennal club, which therefore consists of five segments. The terminal segment is twice as long as it is broad. In the female, the antennal club is more compact and consists of four segments. The terminal segment is no longer than it is broad (fig. 7). For a detailed description of the adults, see Hinton (1945).

T. versicolor is a small oblong-oval beetle measuring 2·5–5 mm. in length and 1·25–2·5 mm. in breadth. Average lengths are male 3 mm. and female 4 mm. (fig. 6). The inner margin of each compound eye shows a definite emargination.

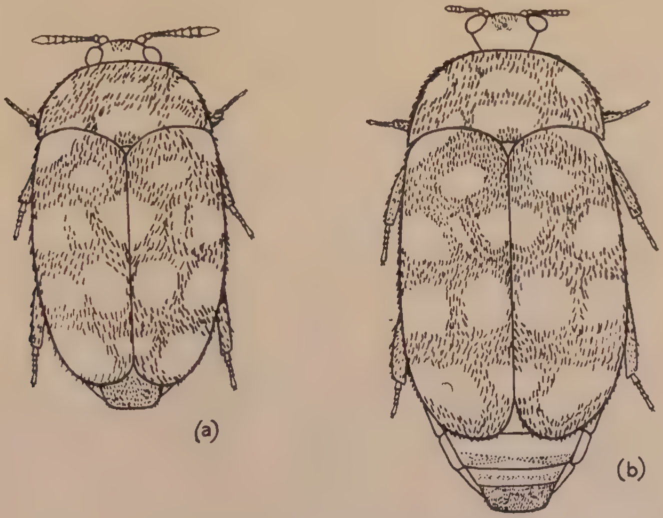


Fig. 6.—Adults of *T. versicolor* (× 16): (a) male; (b) female.

In the male, the antennal club consists of 6 or 7 segments, with the terminal segment twice as long as it is broad. In the female, the antennal club consists of 4 or 5 segments, and the terminal segment is no longer than it is broad (fig. 7). For a detailed description of the adults, see Hinton (1945).

Other morphological differences are shown by dissection of the mouth-parts

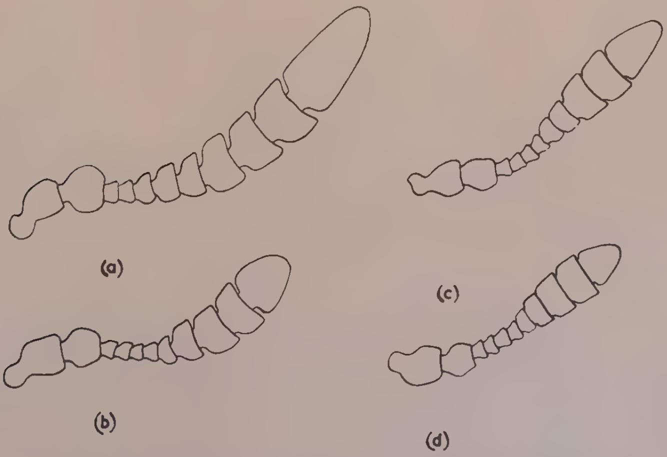


Fig. 7.—Antennae of *T. versicolor*: (a) male; (b) female; and of *T. granarium*: (c) male; (d) female.

and genitalia. The anterior margin of the mentum is deeply emarginate in *T. granarium*, but is much less so in *T. versicolor*. The paired sclerites of the bursa copulatrix in the female are small and bear few teeth in *T. granarium*, whereas in *T. versicolor* they are larger and bear numerous small teeth. The ventral part of the ninth abdominal or ring segment of the male is rounded ventrally in *T. granarium* and is flattened in *T. versicolor*.

The adults do no damage to grain, for normally they do not feed. Norris (1936), working with *T. versicolor*, showed that the adults require neither food nor water for the attainment of their full fecundity and longevity. No free water is required before oviposition will take place. Repeated copulation throughout the oviposition period is unnecessary for the attainment of full potential fertility. A single copulation is sufficient to fertilise all the eggs. Females isolated from the male after starting oviposition lay as many eggs as females left with males throughout life. The rate of oviposition and fertility of the eggs laid also remains unchanged. These facts were also verified for *T. granarium*.

The adults of both species live for only a short time, and the females produce their full complement of eggs within a few days. Copulation will take place immediately after emergence, and is followed by a short pre-oviposition period. The majority of the eggs are deposited during the first few days of the oviposition period; the daily egg number then decreases rapidly. The female lives a few more days, without laying eggs, before death occurs. The abdomen of a newly emerged female is fully extended with the last few abdominal tergites projecting beyond the elytra but, as oviposition takes place, the abdomen shrinks and the elytra finally completely cover the abdomen.

Effects of Temperature and Humidity.

Materials and methods.

Experiments to determine the effects of temperature and humidity on the various stages of the life-cycle were carried out in incubators ranging from 15°C. to 40°C. at 5° intervals.

As the low humidities are of greatest practical interest, and as at high humidities the food material is subject to fungal attack, relative humidities of 73, 50, 25 and 2 per cent. were chosen. The driest condition was obtained by the use of anhydrous calcium chloride together with a stick of potassium hydroxide to take up any carbon dioxide produced; this gave a relative humidity of approximately 2 per cent. The other conditions were obtained by the use of potash solutions of known specific gravity, as described by Buxton (1931).

The potash solutions were placed in desiccators at each temperature, and were left for several days to allow equilibrium to be reached before the commencement of experiments. A paper hygrometer in the desiccator gave an indication of the constancy of this humidity over a period of time. It was found necessary to replace the potash solutions with fresh ones at four- to six-week intervals.

The food material used was brewers' malt which had been kilned at 180–200°F. and which originally had a moisture content of approximately 2·5 per cent.

Five gm. of malt were placed in a 3 × 1 inch specimen tube, and a number of such tubes were placed in each desiccator. The uptake of moisture by the malt from the air within the desiccator, now in equilibrium with the potash solution, was found to be quite fast at first, but then fell off until it was negligible for the purpose of these experiments. It was considered that a week was a sufficient period to allow the malt to come into equilibrium with the air in the desiccator. After this time the food could be used for experimental purposes.

Samples were also taken for the determination of the moisture content of the malt under different conditions. For each determination, approximately 5 gm. of malt were crushed through a grinding mill into an aluminium tin and dried in an electric oven, provided with a fan, for a period of 4 hours at 110°C. (Table I).

TABLE I.

Moisture content of malt (%).

Temperature °C.	Percentage relative humidity			
	73	50	25	2
40	12·61	8·69	5·64	2·10
35	12·79	8·90	5·79	2·19
30	12·95	8·88	5·78	2·45
25	13·17	9·03	5·83	2·36
20	13·01	8·95	5·98	2·29
15	13·76	9·22	5·89	—

Effects of temperature and humidity on oviposition.

Adults were reared under the conditions in which they were used for egg-laying. Each 2 × 1 inch specimen tube contained a newly emerged female and male beetle, together with a folded piece of black paper. The female oviposited in the folds where the eggs were not damaged by movements of the adult beetles. The eggs were counted and removed daily.

Preoviposition period.—The preoviposition period of both species is of short duration, and at any one temperature its length is unaffected by changes in the humidity. At 40°C., the preoviposition period is negligible, copulation and oviposition commencing immediately after emergence of the adults. As the temperature decreases the preoviposition period increases: at 35°C. it is 1 day; at 30°C., 2 days; at 25°C., 2–3 days; and at 20°C. it is greatly lengthened and egg-laying is irregular.

Oviposition period.—Oviposition is completed in a few days, and death of the female follows shortly after. At constant humidity, the oviposition period increases with a decrease in temperature. For instance, at 40°C. oviposition is completed after 3 or 4 days; at 25°C. it extends over a period of up to 12 days. At constant temperatures, the oviposition period is shorter at lower humidities (Tables II & III).

Egg number.—The number of eggs laid by the two species shows a marked difference. Under optimum conditions, that of *T. granarium* is between 30 and 50, and is small compared with the 100 to 120 of *T. versicolor*.

At 40°C., the egg number of *T. versicolor* is small, increasing with a decrease in temperature to a maximum at 30°C., then decreasing with a further reduction in temperature until the adults become inactive below 20°C. Oviposition does not take place under the driest conditions (2% R.H.) at 40° C. and 20°C. but occurs at all humidities at the intervening temperatures. At constant temperature, the egg number increases with an increase in the humidity.

The egg number of *T. granarium* shows little variation at the different temperatures between 40°C. and 25°C. At 20°C. the adults are inactive and produce no eggs. Oviposition occurs at all humidities and again the higher humidities are more favourable.

Fertility.—A small proportion only of the few eggs of *T. versicolor* deposited at the extreme temperatures 40°C. and 20°C. are fertile; these are at the two higher humidities. At the intervening temperatures, hatching takes place at all humidities, and at constant temperature fertility is greater at the higher humidities.

Eggs of *T. granarium* hatch at all humidities in the temperature range between 40°C. and 25°C.

TABLE II.

Egg number and fertility of *T. versicolor.*

Temp. (°C.)	R.H. (%)	No. of females	Mean oviposition period in days	Mean no. of eggs per female	Percentage hatch
40	73	20	1·8	20	13
40	50	20	2·5	31	18
40	25	20	2·5	17	0
40	2	20	0	0	0
35	73	25	4·5	50	74
35	50	25	3·6	55	79
35	25	25	2·6	32	73
35	2	25	2·2	30	62
30	73	25	7·0	109	82
30	50	25	5·6	100	76
30	25	25	4·6	64	58
30	2	25	3·8	54	51
25	73	25	7·7	113	76
25	50	25	7·5	84	78
25	25	25	4·8	52	53
25	2	25	4·1	45	45
20	73	20	8·4	66	50
20	50	20	3·4	20	30
20	25	20	3·2	18	0
20	2	15	0	0	0
15	no eggs laid				

Duration of the egg stage.—Humidity has no apparent effect on the duration of the egg stage. Temperature, on the other hand, influences it to a marked degree. The egg stage of *T. granarium* is prolonged from 4·5 days at 40°C. to 9 or 10 days at 25°C.

Effects of temperature and humidity on length of larval life.

Twenty newly emerged larvae were placed in each 3 × 1 inch glass tube containing 5 gm. of malt conditioned at the required temperature and humidity as described previously. The larvae pupate freely among the grains, usually near the surface, so that the time of pupation was determined easily by daily inspection of the tubes during the period of pupation. Usually the female larva has one more moult than the male and requires a few more days to complete its development than does the male. Details for the two sexes are separated in the results given in Tables V and VI.

The minimum length of larval life of *T. versicolor* is 20 days at 35°C. Above this, at 40°C., larval life is prolonged and is approximately doubled, while the percentage survival is reduced considerably, and none survive the driest conditions. Below this, larval life is progressively lengthened, and at 20°C. is so prolonged that after eight months only a few larvae pupated although other larvae were still alive and apparently healthy. At 15°C. no larvae pupated.

TABLE III.

Egg number and fertility of *T. granarium*.

Temp. (°C.)	R.H. (%)	No. of females	Mean oviposition period in days	Mean no. of eggs per female	Percentage hatch
40	73	20	3·3	38	58
40	50	20	3·3	39	54
40	25	20	3·0	34	60
40	2	20	2·5	23	49
35	73	25	3·6	44	66
35	50	25	3·4	46	75
35	25	25	3·4	29	50
35	2	25	3·0	27	55
30	73	25	5·0	41	58
30	50	25	4·8	41	60
30	25	25	3·9	30	53
30	2	25	2·9	29	51
25	73	25	6·8	43	58
25	50	25	7·5	39	50
25	25	25	5·7	40	52
25	2	25	4·4	25	49
20	no eggs laid				

T. granarium, too, has a minimum larval life, of 15 days, at 35°C. Growth at 40°C. is nearly as quick, and completion of development occurs at all humidities at this temperature. Below 35°C., the length of larval life increases with decrease in temperature. At and below 20°C., the larvae go into a state of quiescence and none had pupated after 12 months. The larvae of *T. granarium* are more resistant to dryness than are those of *T. versicolor*, but both species show a higher rate of development at the higher humidities.

The interpretation of results obtained at different humidities is not straightforward, as more than one factor is involved. The moisture content of the food varies from 2 per cent. at 2 per cent. R.H. to 13 per cent. at 73 per cent. R.H.

TABLE IV.

Duration of egg stage of *T. versicolor*.

Temp. (°C.)	Time in days
40	4·5
35	5·0
30	6–7
25	9–10
20	18–20

TABLE V.

Duration of larval life of *T. versicolor*.

Temp. (°C.)	R.H. (%)	No. of larvae	Percentage pupated	Male		Female	
				Mean length of life in days	Range in days	Mean length of life in days	Range in days
40	73	68	47	53	37–89	84	78–90
	50	79	33	68	48–88	75	43–48
	25	65	19	96	84–112	104	96–112
	2	55	0	—	—	—	—
35	73	150	71	31	20–66	38	25–75
	50	229	87	27	23–47	35	27–63
	25	162	91	40	32–66	51	34–84
	2	40	28	98	90–115	95	83–127
30	73	274	93	31	27–49	38	27–49
	50	167	91	34	29–54	38	29–54
	25	108	69	43	36–63	47	36–63
	2	55	38	68	46–85	81	46–85
25	73	190	78	41	37–59	50	37–59
	50	217	76	48	39–82	55	39–82
	25	100	86	51	45–88	56	45–88
	2	60	0	—	—	—	—
20	73	119	32	191	155–245	238	205–245
	50	84	2	197	195–198	—	—
	25	108	13	263	238–304	262	242–297

TABLE VI.

Duration of larval life of *T. granarium*.

Temp. (°C.)	R.H. (%)	No. of larvae	Percentage pupated	Male		Female	
				Mean length of life in days	Range in days	Mean length of life in days	Range in days
40	73	143	85	22	17–32	24	18–38
	50	117	86	18	15–27	19	16–29
	25	132	79	22	17–34	24	19–33
	2	147	61	35	29–46	38	33–45
35	73	119	92	17	15–21	20	17–25
	50	155	90	19	16–26	21	19–29
	25	166	91	23	18–39	25	20–37
	2	129	65	32	25–47	33	26–49
30	73	120	82	22	19–34	27	21–44
	50	157	89	24	20–51	31	25–56
	25	127	83	27	21–60	33	23–68
	2	112	73	28	24–39	35	26–52
25	73	156	45	33	24–45	36	27–57
	50	70	49	39	31–61	47	33–64
	25	90	38	44	40–65	48	41–63
	2	50	10	60	55–64	68	62–72

(see Table I) and must play an important part in the development and survival of the larvae. This factor probably exerts a greater influence on the rate of development than the relative humidity of the air. The higher rate of development at the higher humidities is accounted for largely by the greater amount of available water in the food.

TABLE VII.

Duration of pupal life.

Temp. (°C.)	Male		Female	
	Length of pupal life (days)	Adult in last larval skin (days)	Length of pupal life (days)	Adult in last larval skin (days)
T. versicolor				
40	3	1	3	1
35	3–3·5	1–1·5	3·5–4	1·5–2
30	4	2	4·5–5	2–2·5
25	6	2·5–3	6–6·5	3–3·5
20	12	5–6	12–13	5·5–6·5
T. granarium				
40	3	0·5–1	3	1
35	3	1	3	1
30	3·5–4	1·5–2	4	2
25	5–5·5	2·5–3	6	3

Effects of temperature and humidity on length of pupal life.

At constant temperature, humidity has no appreciable effect on the duration of the pupal stage, or on the period in which the adult remains in the last larval skin while hardening and pigmentation of the cuticle take place. The length of pupal life increases as the temperature decreases. Figures are given in Table VII.

TABLE VIII.

Mean length of life of males and fertilised females in days.

Temp. (°C.)	R.H. 73%		R.H. 50%		R.H. 25%		R.H. 2%	
	M.	F.	M.	F.	M.	F.	M.	F.
T. versicolor								
40	10	8	9	8	9	8	—	—
35	10	8	11	9	9	7	7	7
30	16	12	13	10	11	9	8	7
25	19	14	17	14	13	11	15	14
20	38	38	38	38	32	34	—	—
T. granarium								
40	5	5	5	5	5	4	4	4
35	6	6	6	5	6	5	4	4
30	10	8	10	8	8	6	6	5
25	16	13	15	13	13	11	12	11

Effects of temperature and humidity on length of adult life.

The adults of both species are short-lived. Males generally outlive fertilised females. At constant humidity, the length of life increases as the temperature falls, until at 20°C. the beetles become inactive and live for a comparatively long period. At constant temperature, lower humidities are less favourable to adult life.

Nutritional Requirements of Larvae.

Experiments were carried out to determine the effects of different foods on the rate of growth of larvae of *T. versicolor*. Eggs were obtained from females kept at 28°C. and 70 per cent. R.H. Ten first-stage larvae were placed in each 2 × 1 inch glass tube on 3 gm. of food conditioned at 28°C. and 70 per cent. R.H. The rate of growth of larvae was determined by measuring the time from hatching to pupation.

In the first experiment, the foods consisted of wheat, malt, maize, fishmeal, dried milk and ground rice. Moisture contents were 6 per cent. for dried milk, 11 per cent. for fishmeal, and 12–13 per cent. for the remainder. Growth occurred equally well on wheat and malt, and was only slightly slower on maize. Pupation of both males and females was completed in 37–47 days on wheat, 38–49 days on malt, and 41–53 days on maize. The other foods were unsatisfactory. Only 25 per cent. of the larvae pupated on fishmeal in less than 70 days, and none pupated on dried milk and ground rice in this time although larvae were still alive but small.

The rates of growth of larvae on flours of different extraction show that there is a critical value of extraction between 85 and 75 per cent. Larvae grew as well on 85 per cent. flour as on wholemeal, pupation being completed in 30–50 days. On the other hand growth was very slow on National Straight Run (75 per cent. extraction) and on Patent Flour (40 per cent. extraction) and no larvae had pupated after 70 days.

Larvae grew well on an artificial diet developed by Fraenkel & Blewett (1943). This diet has the following composition:—

Casein	50
Glucose	50
Cholesterol	1
Dried brewers' yeast	5
Salts (McCallum's mixture)	2

Ten per cent. water is added and thoroughly mixed with the above ingredients to give a 50 per cent. glucose diet. Pupation was completed on this diet in 26–37 days.

Variations on this diet were made up as follows:—

(i) With no carbohydrate,
(ii) With 20 or 80 per cent. glucose instead of 50 per cent. glucose,
(iii) With no cholesterol,
(iv) With wheat germ oil instead of the yeast as a source of B vitamins,
(v) With B vitamins in pure substance instead of the water-soluble yeast fraction.

There was no significant difference in the rate of growth on these various diets. Cholesterol is not an essential constituent of a diet which does, however, contain yeast as a source of other sterols. The presence of B vitamins in sufficient amounts is a factor determining the efficiency of a diet for *T. versicolor* larvae.

Summary.

Two Dermestid beetles, *Trogoderma granarium* Everts and *T. versicolor* (Creutz.) have been recorded on a variety of stored products. In England, *T.*

granarium is a serious pest only in maltings. The life-history is described. The larvae are responsible for the damage to stored products, and their hairy nature facilitates the spread of infestations on sacking and clothing.

All stages in the life-cycle are resistant to heat and dryness.

Optimum temperatures for development are from 30°C. to 35°C. when the life-cycle from egg to adult may be completed in 24 days (*T. granarium*), and 30 days (*T. versicolor*). At temperatures below this optimum, development is much slower and at 20°C. it is so slow that even after 12 months no larvae of *T. granarium* pupated. The use of cool storage would be a possible method of control, for it is not possible for an infestation to develop even after prolonged storage at air temperature.

The duration of the egg and pupal stages is unaffected by changes in the humidity, but higher humidities are more favourable to the development of the larvae. The higher moisture content of the food under these more humid conditions is probably of greater importance than the humidity of the air.

The larvae of *T. versicolor* grow on a variety of food-stuffs with varying degrees of success. Carbohydrate is not essential for normal development, nor is cholesterol if yeast is present as a source of other sterols; the controlling factor appears to be a sufficiency of B vitamins.

Acknowledgements.

I should like to express my thanks to Professor J. W. Munro, Professor O. W. Richards, Dr. G. Fraenkel and Mr. G. V. B. Herford for advice and encouragement, and to the University of London for permission to publish this material from a thesis submitted for the degree of Ph.D. in 1945. I am also extremely grateful to Mr. R. W. Howe for his stimulating interest in the publication of this work.

References.

Arrow, G. J. (1917). Ann. Mag. nat. Hist., (8) **19**, pp. 481–482.

Barnes, J. H. & Grove, A. J. (1916). Mem. Dep. Agric. India, Chem. Ser. **4**, pp. 165–280.

Buxton, P. A. (1931). Bull. ent. Res., **22**, pp. 431–447.

Cotes, E. C. (1893). Indian Mus. Notes, **3**, no. 1, p. 23.

Cotes, E. C. (1894). Indian Mus. Notes, **3**, no. 3, p. 119.

Fraenkel, G. & Blewett, M. (1943). J. exp. Biol., **20**, pp. 28–34.

Ganglbauer, L. (1904). Die Käfer von Mitteleuropa, **4**, p. 36.

Hinton, H. E. (1945). A monograph of the beetles associated with stored products. Volume 1.—443 pp. London, Brit. Mus. (Nat. Hist.).

Lefroy, H. M. (1906). Indian insect pests.—318 pp. Calcutta, Supt. Govt. Printing.

Lepesme, P. (1938). Rev. franç. Ent., **5**, pp. 104–106.

de Lépiney, J. (1930). Mem. Soc. Sci. nat. Maroc., **23**, 100 pp.

Miles, H. W. (1928). Bull. ent. Res., **18**, pp. 251–255.

Nakayama, S. (1931). J. agric. Exp. Sta. Govt-Gen. Chosen, no. 18, pp. 1–24.

Norris, M. J. (1936). J. Anim. Ecol., **5**, pp. 19–22.

Pettit, R. H. (1930). 69th Rep. Bd Agric. Mich., 1929–30, p. 217.

Richards, O. W. (1941). Proc. R. ent. Soc. Lond., (C) **6**, p. 18.

SOLODOVNIKOVA, O. (1937). Acta Univ. Asiae med., (8, zool.) fasc. 41, pp. 1–20.
TWINN, C. R. (1932). Canad. Ent., **64,** pp. 163–165.
VOELKEL, H. (1924). Arb. biol. Reichsanst., **13,** pp. 129–171.
WALKER, J. J. (1917). Ent. mon. Mag., **53,** p. 165.

A METHOD OF MARKING ISOLATED ADULT LOCUSTS IN LARGE NUMBERS AS AN AID TO THE STUDY OF THEIR SEASONAL MIGRATIONS.

By J. T. Davey

*International African Migratory Locust Control Organisation.**

For many years workers have studied the movements of individual adult locusts by marking them, either with paints or by mechanical means (Ramchandra Rao, 1938; Lea, 1953). Although it is comparatively easy to mark locusts, either by hand or by spraying appliances, when swarms or large numbers are present, the problem is very different when populations are scattered and at low density; for some time the lack of a method suited to these conditions seriously hindered studies of the suspected seasonal movements of the African Migratory Locust, *Locusta migratoria migratorioides* (R. & F.), in the solitary phase in the French Sudan (Davey, 1953). The activity of the locusts and the scattered distribution of the small numbers which may be present in their seasonal habitats make hand marking difficult and often impossible, as so much time is wasted in capturing the insects before they can be marked. After a preliminary survey of the problem in 1951, it was decided that in order to mark locusts in large numbers under such conditions it would be necessary to devise a method of marking which did not involve catching them.

Spray Guns and Paints.

In similar work in Nigeria on the flight range of a Tabanid, *Chrysops silacea* Aust., a method of marking that had been used (Shannon, Burke & Davis, 1930) was adopted and modified. The dye used (methylene blue) was sprayed on to the fly through a nasal atomiser or a small flit gun and flies could thus be marked without the undue handling which appeared to have fatal effects (Davey & O'Rourke, 1951). It was considered that a similar method by which a dye or a paint could be applied to individual locusts by means of a small but accurate hand sprayer might be successful.

Experiments were carried out with several different sprayers. The model finally chosen for further trials in the field consisted of a brass reservoir of about two pints' capacity in the top of which is a small hand pump by which the container can be pressurised. The nozzle supplied with the machine was modified by drilling a hole about 1/16th of an inch in diameter through the centre of the swirl plate.† By means of an efficient trigger mechanism, the apparatus can be used to throw accurately a jet of moderately fine droplets a distance of about 15 feet. Untrained assistants can mark settled locusts at this range, and under favourable conditions it was often possible to mark them in flight. At 15 feet, a circle of more than a foot in diameter is covered and any locust in this circle will receive a number of droplets. It is probable that the apparatus could be further improved to give a greater range and a better coverage within the target area. The only disadvantage of it is that the conical rubber washer between the pump and the reservoir (the pump fits into the hole which serves for filling the reservoir and so has to be removed each time the container needs filling) soon becomes misshapen and has to be replaced; it is therefore essential to have some spare washers. A new model is now being produced in which the pump is fitted into the handle and does not therefore need to be removed for refilling. This modification overcomes the disadvantage, but the new model is less robust and as yet it has not been tried in the field.

---

* On secondment from the Department of Agriculture, Nigeria.

† This modification was suggested by Dr. J. E. Hardy, for whose help the writer is indebted.

The paints developed for use in the spray gun to mark the locusts are now obtainable in various colours. Three colours, red, yellow and blue, have been tested in the field and the laboratory, but only the first two were sufficiently apparent on the locusts to be useful. All the paints are suspensions of pigment in light oil. The composition of the red paint supplied for use in the work described here was Rubine Toner B.S., wood rosin and a high-grade kerosene in the proportions 6:6:88. A rather less diluted but otherwise similar paint is now available. The yellow paint consisted of Monolite Yellow G.N.S., wood rosin and kerosene in the proportions 10:20:70.

It was suggested originally that fat-soluble dyes should be used instead of paints but it was decided that none was sufficiently light-fast. The advantage of a fat-soluble dye would be to ensure a certain penetration of the cuticle and so give a more permanent mark. There is little if any penetration of the paints that have been used. Observations made by Mr. B. Nickerson at the Anti-Locust Research Centre on the degree of penetration, showed that the pigment does not penetrate below the chitin layer, and experiments with an artificial cuticle layer (wax on glass) further suggested that little penetration of the wax layer of the integument could occur. During this work, aggregation of the dye on the intersegmental membranes was noted.

When the paints were first supplied, it was suggested that for use they could be diluted with odourless distillate in the proportion of three parts of the diluent to one part of the paint. In West Africa, only commercial kerosene was available; when this was used as the diluent it had definite toxic effects on the locusts, and after preliminary experiments its use was discontinued. The paint has since been used undiluted. This naturally increases the cost of the method

TABLE I.

Length of life of marked and unmarked locusts in cages.

	Unmarked (16♂♂, 12♀♀)	Marked with red paint undiluted (10♂♂, 10♀♀)	Marked with red paint diluted 1 : 3 with kerosene (6♂♂, 6♀♀)	Marked with yellow paint undiluted (10♂♂, 8♀♀)	Marked with yellow paint diluted 1 : 3 with kerosene (6♂♂)
Average life of males (days)	6	9	1	7	3
Average life of females (days)	12	15	2	20	—
Maximum life (days) ..	34	35	5	37	10
Percentage dead after 5 days	56	45	92	50	83
Percentage dead after 10 days	78	55	100	55	83
Percentage dead after 20 days	81	70	100	55	100

and if a less toxic diluent could be found it would be an advantage as even when diluted the paint is still readily visible.

Toxicity of the Paints and their Durability on the Locusts.

As time was a limiting factor, only the most elementary tests on the toxicity of the paint and the duration of persistence of the marks were carried out in the laboratory before the method was used on a large scale in the field. However, the preliminary tests conducted by the manufacturers, using the Desert Locust, *Schistocerca gregaria* (Forsk.), suggested that the paints were in fact of very low toxicity if suitably applied, and when the experiments were brought to an end after seven days the marks were still clearly visible.

The other laboratory trials were carried out in cages in April 1953, at Dogo in the French Sudan with *L. m. migratorioides*, and the results are given in Table I.

The undiluted red paint seems to have no effect on longevity, and in fact the average life after marking of both males and females was a little longer than that of unmarked specimens. The same paint diluted 1:3 with commercial kerosene was much less successful and no adult survived for more than ten days after marking with either paint diluted. Those locusts marked with the undiluted red paint were easily recognisable up to 35 days after marking, when the last one died. The results might appear to suggest that the yellow paint undiluted was equally non-toxic, but in the field there are indications that the yellow is rather more toxic than the red; it is doubtful if this slight difference is significant. The laboratory results with the undiluted paints were supported by the results obtained later in the field, where there were no important adverse effects on the locust populations and few corpses were seen after marking.

Later trials in the laboratory were designed to compare the effects of marking with these paints with the effects of the more usual methods of marking. Both " artists' oil colours " and " fluorescent " paints, applied by hand, were tested and it was found that the special paints applied by the spray guns were the least toxic. Fluorescent paints were almost as good, but artists' oil colours appeared to be more toxic than had formerly been supposed.

The Spray-gun Technique Compared with Hand Marking.

Tests carried out in the field to compare the new technique with hand marking showed invariably that with the spray guns many more locusts could be marked. In November 1952, at a place where the adult locust density was measured as 15 per 100 paces, locusts were marked with a spray gun for one hour, and for the next hour six labourers were engaged in catching locusts which were then marked by hand. With the spray gun, 72 locusts were marked in an hour, but during the next hour the number marked by hand was only 32. The difference per man/hour was therefore very great, 5 or 6 compared with 72. On a second day, at another locality, where there was an adult density measured as 7 to 8 per 100 paces, one gun marked an average of 60 locusts per hour; during the same period six collectors, several of whom were well trained, could bring in only about 100 per hour or 17 per collector.

It should be stressed that the difference between the two methods increases as the adult locust density diminishes. It is at the very lowest densities, when hand marking would be difficult if not impossible, that the spray guns are most useful; they enable the operator to mark sufficient locusts, even at these densities, to permit some hope of recoveries. When densities are high, from 50 to 100 per 100 paces, both the spray guns and collectors can be used to advantage, although one gun may still mark two or three times as many locusts as are brought in by the collectors. In field trials when densities were high, three spray guns and six collectors were used and the greatest number of locusts marked in a morning was 2,271.

The efficiency of the spray-gun technique in the field may, however, be reduced considerably by two factors, thick vegetation and high winds. When the vegetation is thick, it is more difficult to see the locusts when they settle. They are rarely seen quickly enough to mark them when they are first disturbed, but some may be marked in flight. Usually it is best to watch where they settle and then mark them, but if the vegetation is very dense, the spray will not penetrate and the locusts will be only lightly marked. If a locust dives into a dense tuft of vegetation and is not visible it is better to leave it rather than to spray the tuft in the hope that a few droplets will penetrate to where the locust is hiding. This is especially important if an accurate count of the number or percentage marked is required.

When the wind is really strong it is almost impossible to mark with the spray gun. Under such conditions it is equally difficult to mark by hand as the locusts are carried long distances down-wind and few can be captured. With winds of moderate strength it is possible to mark down-wind with the gun, but the jet is not sufficiently powerful to travel far enough into the wind.

A further drawback of the spray-gun technique is that the amount of paint used is much greater than when marking is done by hand. Apart from the higher cost, there is also the problem of obtaining the large quantity of paint needed and transporting it to the isolated areas where locust studies are necessarily carried out. The actual difference in cost will depend to a great extent on the local cost of labour. Using the spray gun, it is possible for one man to mark 400 locusts in a day under normal conditions and for this about 1½ gallons of paint would be needed. The approximate cost of the paint is 30*s.* per gallon and the cost of labour in French West Africa 3*s.* 6*d.* per day, so that the cost of each marked locust is about 1·5 pence. It would take four collectors to catch the same number of locusts in a day for hand marking, and as the cost of the paint used in hand marking is almost negligible the total cost is about 0·4 pence per locust.

Results obtained by Marking in French West Africa.

In the autumn of 1953, marking on a very large scale was carried out in the French Sudan to investigate the suspected seasonal movements of solitary individuals of *L. m. migratorioides.* It was not possible to mark locusts throughout the whole of the vast area involved in these movements, but certain well-defined habitats were chosen which contained the greatest number of adults. In some habitats the densities exceeded 100 per 100 paces. As the object was to mark as many as possible and supplies of paint were limited, both hand marking and the spray guns were used. In a little over two months, some 53,000 adult locusts were marked. Each operator carried a hand counter to record the number marked by him. Only one colour, red, was used.

The spray guns worked well throughout the operations and there were no mechanical troubles except for the washers already mentioned, which needed renewing after the first three weeks. There was no trouble from clogging; the guns were washed through each evening with kerosene. The maximum number of locusts marked in any one habitat was 10,133 and it was estimated that in the most successful experiment 51 per cent. of all locusts in the habitat had been marked.

At one locality (Dioura), three operators with spray guns and six permanent collectors were used. After a little practice this team would normally mark about 250 locusts each hour and on one occasion more than 2,200 were marked between 0800 and 1300 hrs., *i.e.*, 440 per hour. The paint appeared to have little effect on the locust populations although after several mornings' spraying in the same habitat large patches of the vegetation would be stained red. The few corpses recovered indicated that the mortality rate after marking was very low; some of the locusts were so heavily sprayed that they could be easily recognised in flight. A few which were caught some days after marking, still living normally, had the tips of the elytra frayed suggesting that they had tried to scratch off the paint, but most of these had been heavily over-sprayed. It is possible that this mechanical injury would be a handicap on migrations over long distances. Only 12 corpses were recovered and these were dissected. In all cases the paint had reached the internal organs, especially the crop and foregut, which consequently were stained. In most cases it appeared to have been ingested (possibly with the stained vegetation which may have been eaten by the locusts, though this seems unlikely), and there was little indication that any paint had been taken in through the cuticle or spiracles.

Many of the marked locusts were captured later in the localities where they had been marked and four that had been marked in semi-arid country were recovered on the flood plains of the Niger. Thus, proof was obtained that migrations of solitary locusts over long distances are possible. The distance travelled by each of these four locusts was at least 60 kilometres, and as there is some evidence that a circuitous route was followed during this migration the distance may have been much greater. The last marked locust to be recovered was taken some five weeks after marking, showing that in the field the marking lasted at least as long as in cages. It is not surprising that only four marked locusts were recovered after such long migrations. By marking and capturing later it was possible to estimate approximately the numbers of locusts present in the comparatively few habitats where marking had taken place. In these habitats adult densities varied from 300 to 2,000 per hectare and when it is realised that similar habitats in which no marking was possible are scattered throughout an area of more than 600,000 hectares it is apparent that only a very small fraction of the total population could have been marked.

Possibilities of Improving present Marking Techniques.

As the work in the French Sudan is by no means finished, the search continues for an even better technique of marking locusts in large numbers when populations are scattered. There is little doubt that the spray gun itself could be improved to give greater range and greater accuracy. The spray-gun technique eliminates only the necessity of capturing the locusts for marking them; it is still necessary to capture them to see if they are marked, except in cases of exceptionally distinct or recent marking. During the 1953 experiments in the French Sudan, this was an important factor militating against the success of the marking campaigns. Although 53,000 locusts were marked, only 10,000 were later captured during the search for marked specimens. This great difference in numbers reflects the much lower densities present in the new habitats to which the locusts migrate, and also the greater difficulty in collecting in habitats such as the flooded plains of the Middle Niger. It is therefore desirable to find a method such that both the marking of the insects and the subsequent recognition of those marked can be carried out without capturing them. Fluorescent paints may be useful in this connection, and some preliminary experiments have already been made in the hope that they might be visible on locusts at night in a beam of either white or ultra-violet light. In cages these paints were proved to be relatively non-toxic to the insects but those tested were not as visible by night as had been hoped. They were not tested under ultra-violet light as no portable source of it was available. It is hoped to continue experiments with fluorescent paints as they may yet solve the problem of recognising marked locusts without capturing them.

Summary.

A method of marking adult locusts, particularly useful when numbers are low and hand marking would be difficult, is described. It involves the use of a small hand spray gun from which a jet of paint can be directed at the locusts in spurts at ranges up to about 15 ft. The paints tested consisted of suspensions of pigments in light oil.

The paints are of low toxicity and the marks remain visible for many weeks. By the use of this method far more locusts can be marked in a given time than could be marked by hand. The efficiency of the method is reduced by high winds and dense vegetation, and it is more costly than hand marking. Most of the marked locusts cannot be recognised as such without being captured.

Some results obtained with this method in the French Sudan are given. In two months more than 50,000 locusts, *Locusta migratoria migratorioides* (R. & F.), were marked with a red paint; four were recovered 60 kilometres or more from the area in which they were marked, and the paint was clearly visible after five weeks.

Ways of improving the technique, and other possible methods of marking, are discussed.

Acknowledgements.

This work was carried out on behalf of the Provisional International Committee for Locust Prevention in the French Sudan.

The writer wishes to thank Dr. B. P. Uvarov and Dr. B. Zolotarevsky for their helpful criticism and advice, and the several assistants who contributed to the field work. He is also indebted to Mr. M. Roblot, Director of the " Aire Grégarigène " on the Middle Niger, for the material aid so readily given. The helpful co-operation of Imperial Chemical Industries and Monitor Engineering and Oil Appliances Ltd. is also acknowledged, the former having produced the paints and tested them on locusts in the laboratory and the latter being the makers of the spray guns used.

References.

Davey, J. T. (1953). Possibility of movements of the African Migratory Locust in the solitary phase and the dynamics of its outbreaks.—Nature, Lond., **172**, pp. 720–721.

Davey, J. T. & O'Rourke, F. J. (1951). Observations on *Chrysops silacea* and *C. dimidiata* at Benin, Southern Nigeria. Part II.—Ann. trop. Med. Parasit., **45**, pp. 66–72.

Lea, A. (1953). Studies on the behaviour of adult Brown Locusts in the Karoo . . .—Sci. Bull. Dep. Agric. S. Afr., no. 344, 21 pp.

Ramchandra Rao, Y. (1938). A further note on studies of migration among the solitaries of locusts in N.-W. India 1936–1938.—C.R. V^{e} Conf. int. Rech. antiacrid., Brussels 1938, pp. 238–247.

Shannon, R. C., Burke, A. W. & Davis, N. C. (1930). Observations on released *Stegomyia aegypti* (L.), with special reference to dispersion.—Amer. J. trop. Med., **10**, pp. 145–150.

FUMIGATION TRIALS WITH ETHYLENE DIBROMIDE FOR THE CONTROL OF EGGS AND LARVAE OF *CERATITIS CAPITATA* (WIED.) IN *CITRUS* FRUIT.

By A. Grunberg, Ph.D., K. Polac'ek, Dr.Eng. and J. Peleg, Ph.D.
Ministry of Agriculture, Division of Plant Protection, Jaffa.

The population of the Mediterranean Fruit-fly (*Ceratitis capitata* (Wied.)) is subject to considerable fluctuation in Israel, with consequent changes from year to year in the degree of damage caused to *Citrus*, but it must be regarded as a serious pest of that crop. In the last few years the *Citrus* industry has suffered heavy losses from fruit-fly attack; during 1950–51, and again during 1952–53 hundreds of thousands of cases of fruit were disqualified for shipping and still larger quantities decayed in the groves. Furthermore, the pest is a limiting factor in the case of new plantings of late varieties, such as Valencia, which are usually infested. *Citrus* fruits, whatever the variety, remaining on the tree after the first half of March are usually subject to severe infestation.

Control experiments have been carried out in Israel for some time with considerable success, but the primary aim has been the destruction of the adult fly. Without entering into the details of the biology of the Mediterranean Fruit-fly, it may be mentioned that the activity of the adults in *Citrus* groves is largely confined to periods of unsettled climatic conditions, which interfere seriously with control treatments. The possible shortcomings of the control measures tried out necessitated the development of additional methods for the destruction of the eggs and larvae. The need to ship the fruit to world markets in fair condition, free from fruit-fly larvae and secondary decay, in accordance with international standards, suggested fumigation of the fruit with ethylene dibromide.

Ethylene Dibromide Fumigation of *Citrus* Fruits.

Balock (August, 1951) published a paper on the elimination of fruit-fly infestation in fruits and vegetables with ethylene dibromide. Lindgren & Sinclair (December, 1951) published further work on the tolerance of *Citrus* fruits to fumigants effective against the Oriental Fruit-fly (*Dacus dorsalis* Hend.). Lindgren & Sinclair (1953) summed up the results obtained with ethylene dibromide and ethylene chlorobromide. The work of these authors proved that ethylene dibromide was very active in destroying eggs and larvae of the Oriental Fruit-fly; indeed, it was shown to be more active than any other fumigant tested by them, a concentration of 0·5 lb. per 1,000 cu. ft. at a temperature of 70°F. and exposure of 2½ hours being found to give satisfactory control. The results also showed that the fruit was uninjured, the aroma unchanged, and that no off-flavour of the juice was noticeable; the length of storage also had no significant effect. Finally, the bromine absorption and retention in the peel and pulp of the fruit were examined and the concentration was found to be so low that the fumigated fruit was considered safe for human consumption. A Law promulgated by the United States authorities (U.S. Bureau of Entomology & Plant Quarantine, 1951) makes it compulsory for certain fruits and vegetables exported from Hawaii to the United States to be fumigated with ethylene dibromide.

The work of Lindgren and his co-workers seemed to be of great interest in connection with the export of *Citrus* fruit from fruit-fly infested areas in Israel. Soon after the first report on ethylene dibromide fumigation was made public in

1951, a programme of experiments, aiming at the adaptation of the method to local conditions, was designed and put into effect by the Division of Plant Protection.

Tolerance of Jaffa Oranges and local Varieties of Grapefruit to Fumigation.

In the first stage of our experiments the tolerance of Jaffa and Valencia oranges and grapefruit, at different degrees of maturity, to fumigation with ethylene dibromide was investigated. For this purpose galvanised tin containers of 15·5 cm. diameter and 18 litres capacity were used. Ten fruits were placed on the bottom of each container. A tripod, covered with blotting paper, was introduced and a lid was fixed which was sealed with paraffin wax. In the centre of the lid was a small orifice closed with a stopper. With the aid of a micropipette, ethylene dibromide was applied to the blotting paper and the orifice closed. It was found that, at temperatures ranging between 15° and 23°C., the time required to evaporate 90 per cent. of the liquid was 18 to 35 minutes. After 2½ hours the fruits were removed and kept in the open at a temperature of 20°C.; at this temperature the first signs of injury by overdosing appeared after four days; at a temperature of 15°C., damage was noted only after five or six days.

Injury caused by ethylene dibromide fumigation consists of deep-pitted spots on the fruits varying from a few square millimetres to relatively large areas. These blemishes are caused by the breakdown of the oil glands and cellular tissues; in oranges they are brown in colour and in grapefruit reddish brown, turning brown later. The effect of various concentrations of ethylene dibromide on the peel of Jaffa oranges is shown in Table I.

TABLE I.

Tolerance of Jaffa oranges to various concentrations of ethylene dibromide.

Date of treatment	Temp. (°C.)	Concentration (gm./m.^{3})	No. of fruits		Condition of fruit, days after treatment
			Fumigated	Unfumigated (check)	
3.xii.51	16·7	5	25		41 unchanged
,,	16·7	10	25		41 ,,
,,	16·7	20	25		41 ,,
,,	16·7	—	—	25	41 ,,
16.xii.51	15·2	35	10		7 damage conspicuous
,,	15·2	50	10		7 ,,
,,	15·2	75	10		7 ,,
,,	15·2	—	—	10	7 unchanged
26.xii.51	15·5	35	10		4 damage conspicuous
,,	15·5	50	10		4 ,,
,,	15·5	75	10		4 ,,
,,	15·5	—	—	10	4 unchanged
2.i.52	16·0	30	90	5	damage conspicuous
,,	16·0	—	—	10	5 no damage
4.i.52	15·5	20	135		9 ,,
,,	15·5			15	9 ,,
8.i.52	15·1	20	135		6 ,,
,,	15·1			15	6 ,,
10.i.52	15·6	10	135		6 ,,
,,	15·6			15	6 ,,

Exposure to treatment 2·5 hours at 15·1° to 16·7°C.

The absorption and subsequent release of the gas from the fumigated fruits was demonstrated in the laboratory by fumigating some oranges with ethylene dibromide at a concentration of 25 mg./l. After fumigation the fruits were aerated for 15 minutes and placed separately in half-litre glass jars. Subsequently rice weevils (*Calandra oryzae* (L.)) were introduced into the jars and all were found dead after 14 hours.

The fruits were examined at regular weekly intervals; observations were discontinued after 41 days. At a temperature of 15°C., damage became evident after four or five days. Later it was found that, if the fruits showed no signs of damage by the end of the first week, it would remain practically unblemished.

It became evident from this series of experiments that Jaffa oranges have a high ethylene-dibromide tolerance—up to 20 gm./m.^{3} It was learned in later experiments, however, that there is no need for such a high concentration to kill larvae of *Ceratitis*.

Observations on commercially fumigated fruit subsequently justified these conclusions in respect to Jaffa and Valencia varieties; it was found, however, that grapefruit was more sensitive and that 15 gm./m.^{3} is the maximum dose tolerated.

Effect of Fumigation on the Eggs and Larvae of *Ceratitis capitata.*

Having established the concentrations of ethylene dibromide that the principal local varieties of *Citrus* would tolerate, it was necessary to determine the action of the fumigant on the eggs and larvae of *Ceratitis capitata* feeding inside the fruits. The results of some tests, carried out in the apparatus described on p. ~~84~~, are summarised in Table II.
804

TABLE II.

Action of ethylene dibromide on larvae in grapefruit.

Ser. no.	Date of treatment	Date of examination	Concentration (gm./m.^{3})	Temp. (°C.)	No. of larvae living	No. of larvae dead	% kill
1	6. i. 52	10.i.52	5	15·7	39	31	44·3
2	26.xii.51	1.i.52	10	15·5	—	24	100
3	30.xii.51	4.i.52	10	15·6	—	—	—
4	6. i. 52	10.i.52	10	15·7	—	30	100
5	27.xii.51	2.i.52	20	15·2	—	15	100
6	30.xii.51	4.i.52	20	15·2	—	4	100
7	27.xii.51	2.i.52	30	15·2	—	2	100
8	30.xii.51	4.i.52	30	15·2	—	—	—

Exposure to treatment 2·5 hours.
Each series contained 10 to 15 grapefruit.

In nos. 3 and 8, above, the fruit before treatment showed numerous oviposition punctures but, as no larvae were subsequently found in these fruits, either the eggs had been killed or the newly hatched larvae had clearly failed to penetrate into the pulp.

These figures indicated that a high percentage of the larvae could be killed by fumigation with ethylene dibromide.

The results of these preliminary laboratory tests were considered sufficiently satisfactory to justify experiments on a large scale, which were subsequently carried out under field conditions with units consisting of hundreds of cases of loose or packed and wrapped fruits. As it was technically impossible to check such large quantities of fruit in detail, only samples were examined. Fruits for examination were put into specially marked boxes interspersed among the stack of boxes to be fumigated in such a way as to provide representative samples of the entire mass. The boxes in the field experiments were stacked in four layers, the bottom layer being placed on planks 7 cm. above the soil. A gap of a few centimetres was left between boxes to ensure proper circulation of gas and the stack was covered with a rubber-impregnated tent. Each stack consisted of approximately 200 cases of either loose Jaffa oranges or grapefruit. In each stack there were six or seven sample cases and every fruit in one or two of these cases was examined after treatment. The requisite dose of ethylene dibromide was soaked up in a wick that was fastened opposite a small fan so that the air current would accelerate evaporation and cause the heavy fumes to be thoroughly circulated. The temperature was recorded inside the tent by means of a thermograph and a constant temperature of 16° to 18°C. was maintained. Exposure lasted for 2½ hours, and experimental doses of 10, 15 and 25 gm./m.^{3} were tested. The insecticidal and phytocidal effects of these experiments are shown in Table III.

TABLE III.

Effect of varying the concentration of ethylene dibromide on the mortality of larvae in Jaffa oranges and grapefruit.

Date of		Concentration gm./m.^{3}	No. of larvae*		% kill of larvae	Remarks
treatment	examination		living	dead		
24.i.52	29.i.52	10	39	38	49·3	Jaffa oranges
,,	1.ii.52	10	19	16	45·7	,, ,,
,,	29.i.52	15	9	30	76·9	,, ,,
,,	1.ii.52	15	14	36	72	,, ,,
6.ii.52	12.ii.52	20	7	28	80	Grapefruit, 12·4% injured†
7.ii.52	,,	25	10	37	78·7	Grapefruit, 21·9% injured†
24.ii.52	29.i.52	untreated	54	6		Natural mortality in one box, 10%

Exposure time 2·5 hours.

* The figures are the result of the examination of one sample case in each instance.

† The figures given here are for the percentage damage caused by fumigation in 6 sample cases.

The following conclusions can be drawn from the above Table:—

(1) All conditions being equal (material, temperature, concentration and exposure), there were no substantial differences in the results obtained by the laboratory tests and small field experiments.

(2) An increase in gas concentration from 10 gm./m.^{3} to 15 gm./m.^{3} raised larval mortality considerably, but a gas concentration of 20 gm./m.^{3} did not give a significantly higher mortality than 15 gm./m.^{3}, remaining at approximately 80 per cent. This is probably due to a higher absorption of the gas by the soil.

(3) A dosage of 25 gm./m.^{3} of ethylene dibromide did not cause injury to Jaffa oranges.

Summing up the 1951–52 experiments, it was found that, within the limits of 15 to 20 gm./m.^{3}, an exposure of 2½ hours destroyed up to 80 per cent. of the larvae found inside the fruits, packed in the standard way for export, without injury either to Jaffa or Valencia oranges. Grapefruit was shown to be more sensitive and 15 gm./m.^{3} for 2½ hours was considered the safety limit.

These 1951–52 results were considered sufficiently encouraging to continue the experiments and to adjust the fumigation techniques to prevailing conditions in packing houses in order to save additional expenditure.

It is the common practice in Israel to treat *Citrus* fruit before shipping with Decco (NCl_3) against certain fungus diseases. Fumigation chambers are available at all important railway stations. These Decco fumigation chambers are generally well suited to ethylene-dibromide fumigation but whilst the Decco treatment requires six hours' exposure to the gas, 2½ hours is sufficient for the ethylene-dibromide treatment.

As the two gases, NCl_3 and ethylene dibromide, are compatible, simultaneous treatment was thought feasible, provided a suitable dosage of the latter could be established. It was obvious that ethylene dibromide at a concentration of 15 gm./m.^{3} for six hours would cause injury to the fruit. It was necessary, therefore, to find the lowest concentration that would give a satisfactory kill at an exposure of six hours as well as the reciprocal relations of the two gases and their combined influence on the different varieties of *Citrus* at different degrees of maturity.

The fumigation chambers in which the experiments were carried out have a capacity of 600 m.^{3} into which 3,000 boxes of *Citrus* are usually placed. The chambers are built of brick, the ceiling of plywood. There are two large doors in the front wall, enabling the entry of loaded trucks into the chamber, and four smaller doors in the rear wall leading directly on to the railway platform. All doors were closed during treatments. To ensure satisfactory fumigation with Decco, a refilling system is installed whereby additional gas can be supplied to compensate for leakage; in the case of ethylene dibromide no such arrangements were made, and therefore it was very important to keep the chambers hermetically sealed.

The boxes containing the fruit were arranged in such a manner as to allow free circulation of gas, and in order to bring about this circulation, large fans were employed. Containers of ethylene dibromide were placed above the boxes and heated by means of electric stoves.

As, however, the fumigation experiments in the 1951–52 season had been carried out on a small scale, it was thought desirable, before starting a new series of experiments, to verify the data already obtained.

For this purpose a large-scale experiment with 2,400 cases of wrapped fruit, packed in standard boxes, was carried out. The boxes were placed in a fumigation chamber, of the kind described above, and arranged in groups 60 cm. distant from each other and from the walls, in order to allow free circulation of gas. Above the boxes, three containers of ethylene dibromide were placed on three electric stoves; the concentration of gas was 14·7 gm./m.^{3} and the temperature 19°C.; exposure time was 2½ hours. As it would be technically impossible to examine 2,400 boxes, seven boxes, containing specially selected infested fruits, were interspersed in the mass at various points in the chamber and examined after treatment. The results of the examination are summarised in Table IV and confirm the results obtained in the earlier, small-scale experiments.

These 2,400 boxes, sent to the United Kingdom under normal shipping conditions, arrived in good condition. A number of boxes from this shipment was examined by the Phytopathological Service of the United Kingdom and found to be entirely satisfactory from a commercial point of view. To quote from a report by Dr. Moore, of the Plant Pathology Laboratory, Harpenden:

> "The ten cases of oranges fumigated with ethylene dibromide were delivered by the Citrus Marketing Board (London) on 16th January. The oranges were examined here for signs of damage and the presence of insects. They appeared to be in excellent condition and did not show blemishes or discoloration. Their flavour was good. Unfortunately only one orange contained fruit-fly larvae, so we were unable to judge the effect of the treatment."

The boxes in a fumigation chamber are placed in three layers one upon the other; in Table IV, therefore, layer 1–2–3 indicates the position of the box, whether it was on the bottom, middle or top, respectively, of the fumigation chamber.

TABLE IV.

	Box no. 1 layer 1	Box no. 2 layer 3	Box no. 3 layer 2	Box no. 4 layer 2	Box no. 5 layer 1	Box no. 6 layer 3	Box no. 7 layer 2	Totals
Dead larvae	26	25	25	19	—	9	26	130
Living ,,	—	—	33	4	—	—	—	37

Fruit fumigated on 24.xii.52; examined on 29.xii.52.

Low Dosage and Long Exposure Ethylene-dibromide Treatment.

In order to adjust the dosage of ethylene dibromide to conditions of Decco fumigation, it was necessary to investigate the phytocidal and insecticidal effect of low dosage and long exposure on fruit infested with larvae of *Ceratitis capitata*. The fruit was packed in standard boxes and fumigated in fumigation chambers.

The observations on the phytocidal effect are summarised in Table V and on the larval kill in Table VI.

TABLE V.

Phytocidal effect of long exposure of Jaffa oranges to ethylene dibromide.

Date of		No. of fruits	Concentration (gm./m.^{3})	Temp. (°C.)	Phytocidal effect
treatment	examination				
16.xi.52	18.xi.52	14	20	22	Moderate pitting in all fruit
,,	,,	14	16	22	,, ,, ,, ,, ,,
,,	,,	14	12	22	,, ,, ,, ,, ,,
,,	,,	14	Untreated	—	No injury
17.xi.52	19.xi.52	14	20	21–22	Moderate pitting in all fruit
,,	,,	14	16	21–22	,, ,, ,, ,, ,,
,,	,,	14	12	21–22	,, ,, ,, ,, ,,
,,	,,	14	12	21–22	,, ,, ,, ,, ,,
,,	,,	14	Untreated	—	No injury
21.xi.52	30.xi.52	15	10	20·5–21	Slight pitting
,,	,,	15	8	20·5–21	No injury
,,	,,	15	6	20·5–21	,, ,,
,,	,,	15	Untreated	—	,, ,,
25.xi.52	2.xii.52	15	10	20·5–21	Slight pitting
,,	,,	15	8	20·5–21	,, ,,
,,	,,	15	6	20·5–21	No injury
,,	,,	15	Untreated	—	,, ,,

Exposure, 6 hours.

Preliminary laboratory experiments with Decco (NCl_3) showed no influence upon larval mortality of *Ceratitis*, and the next step was to study the phytocidal and insecticidal effects of a combined treatment of Decco and ethylene dibromide upon eggs and larvae of the *Ceratitis* in fruit under normal shipping conditions.

For this purpose 10 to 12 boxes, specially marked and containing infested fruits, were interspersed among 3,000 export boxes to be fumigated. After treatment, the marked boxes were removed for laboratory examination of larval kill. These experiments were carried out on several occasions and at various fumigation plants. As a result, the standard dosage was fixed at 6 gm./m.^{3} ethylene dibromide at 21°C. and 6 hours' exposure, combined with the normal Decco concentration. When the temperature dropped by 3°C., the dosage was increased by 1 gm./m.^{3} ethylene dibromide. The degree of fruit maturity varied considerably according to the dates of treatment. The results are given in Table VII. It is evident from these results that, at a concentration of 6 gm./m.^{3} of ethylene dibromide in addition to the normally applied NCl_3 (Decco) gas, a commercially satisfactory larval kill of up to 94·5 to 98·5 per cent. of *C. capitata* was achieved under ordinary conditions. In some instances (nos. 4 and 6) the kill was less satisfactory but this is explained by unsatisfactory conditions in the fumigation plants which permitted excessive leakage of gas.

TABLE VI.

Effect of long exposure to ethylene dibromide on larval mortality in Jaffa oranges.

Date of		Concentration (gm./m.^{3})	Temp. (°C.)	Exposure (hours)	No. of larvae		% kill
treatment	examination				living	dead	
30.xii.52	4.i.53	10	18	6	—	73	100
”	”	8	18	6	—	87	100
”	”	6	18	6	3	43	93·5
”	”	Untreated	18	—	22	—	—
31.xii.52	5.i.53	10	18	6	—	76	100
”	”	8	18	6	4	106	96·4
”	”	6	18	6	—	17	100
”	”	Untreated	18	—	88	—	0
6.i.53	11.i.53	6	18·5	2·5	13	60	82·2

Ten fruits at each treatment.

No special difficulties arose in the application of the combined ethylene dibromide and Decco treatments. In Israel, Decco applications usually start late in winter, and therefore no expenditure additional to the cost of the ethylene dibromide is involved. The cost of the ethylene-dibromide fumigation of *Citrus* fruit amounts to approximately $4 per ton, somewhat more or less, depending upon the extent of fumigation practice.

Bromide Residue in *Citrus* Fruit after Fumigation with Ethylene Dibromide.

An examination of fruit fumigated with ethylene dibromide for bromide residues was carried out both in Israel and in the United Kingdom, by Dr. Bondy, of the Rehovoth Agricultural Station, and by Dr. Page, of the Imperial College of Science Field Station, Silwood Park, respectively.

Dr. Bondy found a bromide concentration in the skin of from 2 to 15 parts per million and in the pulp of 0·5 p.p.m. These concentrations are considered harmless. The content found by Dr. Page indicated that there was practically no additional bromide, either fixed or volatile, in the pulp; in the skin there was a very small amount of additional bromide, but not sufficient to constitute a danger to workers who handle the fruit.

During the 1952–53 export season, over 160,000 cases of fruit were treated with ethylene dibromide and Decco and shipped to the United Kingdom; no

TABLE VII.

Combined fumigation with ethylene dibromide and Decco, 1953.

Serial no.	Date of		Locality of fumigation plant	Variety of fruit	Number of larvae		% kill	Effect of fumigation on fruit
	treatment	examination			living	dead		
1	24.xii.52	30.xii.52	Rehovoth	Jaffa	37	130	77·8	No fruit injury
2	20.i.53	25.i.53	,,	Jaffa and grapefruit	19	247	94·5	,, ,, ,,
3	22.i.53	26.i.53	Lydda	,, ,, ,,	57	464	88	,, ,, ,,
4	29.i.53	2.ii.53	Yibne	,, ,, ,,	189	401	66·9	,, ,, ,,
5	29.i.53	2.ii.53	,,	Grapefruit	29	—	—	Untreated
6	24.ii.53	9.iii.53	Lydda	,,	16	34	68	No fruit injury
7	25.ii.53	9.iii.53	Rosh-Haayin	Jaffa and grapefruit	1	69	98·5	,, ,, ,,
8	29.ii.53	13.v.53	,,	Valencia	—	—	—	,, ,, ,,
9	29.ii.53	13.v.53	,,	Grapefruit	—	—	—	Untreated—3·7% slightly blemished

Exposure 6 hours; dosage 6 gm./m.^{3}

Remarks: The number of cases in each serial number varied between 2,000 and 3,000 standard boxes. From each block treated six or seven boxes were selected and all the fruits in them, totalling about 1,000, were examined. The figures under "Number of larvae" are for the total found in these 1,000 fruits.

Nos. 4 and 6 suggest unsatisfactory fumigation conditions.

In Nos. 8 and 9 only the effect upon the quality of the fruit in relation to its maturity was studied.

The number of untreated cases in Nos. 5 and 9 was 7.

complaints were received from the fruit brokers at the port of arrival, either of fruit-fly infestation or of skin blemishes.

During 1953–54 over 500,000 cases, similarly treated, were shipped to the U.S.S.R., and no complaints have been received.

Summary.

Experiments in the treatment of *Citrus* fruit by fumigation with ethylene dibromide for the control of the damage caused by the Mediterranean Fruit-fly (*Ceratitis capitata* (Wied.)) were conducted during 1951–52 and 1952–53.

Jaffa and Valencia oranges were found to tolerate a concentration of 18 gm./m.³ at approximately 20°C. and exposure time of 2½ hours.

Grapefruit was found to tolerate a concentration of 15 gm./m.³ at approximately 20°C. for 2½ hours' exposure. When the exposure time is prolonged to 6 hours the maximum tolerance is 8 gm./m.³

A kill of 75 per cent. of the larvae of *Ceratitis* inside the *Citrus* fruits was obtained by exposure for 2½ hours at a concentration of 15 gm./m.³

Citrus fruit for export from Israel is normally fumigated with Decco (NCl_3) against certain fungus diseases. The exposure in this case is 6 hours. The possibility of combining the treatment with Decco and ethylene dibromide was examined. It was found that the treatments were compatible and that, at an exposure of 6 hours, a dosage of 6 gm./m.³ of ethylene dibromide gave a kill of up to 93·5 to ~~98·4~~ per cent. /100 teste J.W.

Fumigation of fruit for export, in batches of 3,000 cases at a time, showed that 6 gm./m.³ of ethylene dibromide (all other conditions being equal) killed up to 98·5 per cent. of *Ceratitis* larvae (provided no gas leakage occurred in the fumigation chamber). This concentration did not cause injury to Jaffa and Valencia oranges. In the case of grapefruit, slight damage occurred—especially in over-ripe fruit (during the second half of April) which was not intended for shipping.

References.

BALOCK, J. W. (1951). Ethylene dibromide for destroying fruit fly infestations in fruits and vegetables.—Science, **114**, p. 122.

BALOCK, J. W. & LINDGREN, D. L. (1951). Toxicity of various compounds as fumigants to eggs and larvae of the Oriental Fruit Fly.—J. econ. Ent., **44**, pp. 657–659.

LINDGREN, D. L. & SINCLAIR, W. B. (1951). Tolerance of citrus and avocado fruits to fumigants effective against Oriental Fruit Fly.—J. econ. Ent., **44**, pp. 980–990.

LINDGREN, D. L. & SINCLAIR, W. B. (1953). Effect of ethylene dibromide and ethylene chlorobromide fumigation on citrus and avocado fruits.—J. econ. Ent., **46**, pp. 7–10.

U.S. BUREAU OF ENTOMOLOGY & PLANT QUARANTINE. (1951). Ethylene dibromide fumigation approved as a condition for certification of certain fruits and vegetables under Hawaiian Fruit and Vegetable Quarantine No. 13.—B.E.P.Q. 592, 2 pp.

SOME EFFECTS OF THE BRITISH CLIMATE AND CONSTANT TEMPERATURES ON THE LIFE-CYCLE OF *EPHESTIA CAUTELLA* (WALKER).

By H. D. Burges

Ephestia cautella (Wlk.), the " Almond Moth " or " Dried-currant Moth ", is a serious pest only in warm and hot countries. It is continually being imported from these countries into Great Britain on a wide range of foodstuffs (Freeman, 1948). In the British Isles breeding can occur during summer, but it is doubtful if the species is often able to overwinter. This work was undertaken to investigate the problem of overwintering and to examine the possibility of using susceptibility to cold as a method of control. Laboratory experiments were carried out to determine the resistance of the species to constant low temperatures. In addition, during the winters of 1949–50 and 1950–51, experiments were performed at uncontrolled temperatures in various unheated outbuildings at the Pest Infestation Laboratory, Slough, to discover if any individuals could survive those particular winters.

Because the insectary stock of moths available was insufficiently virile, new stocks were obtained by collecting moths from the following products on ships in British ports:—

Stock	I	from	Australian wheat
,,	II	,,	West Indian cocoa
,,	III	,,	Argentine pollards
,,	IV	,,	Cotton seed, origin unknown
,,	V	,,	East African copra
,,	VI	,,	South African groundnuts.

A number of the initial moths collected from ships were used to provide eggs directly for some experiments. In order to provide insects for other experiments, cultures were made with the remaining moths either at 20°C. and 50 to 70 per cent. R.H., or at 25°C. and 70 per cent. R.H. Each culture was formed by placing moths on one to two inches of wheatfeed plus 5 per cent. (by weight) of glycerine in a 7 lb. jam jar. Cultures were destroyed after producing one generation of adults which were used for new cultures. Insects for experiments were bred in this manner for periods of not more than two years.

The density of breeding cultures obtained varied considerably. Since the population density during growth may seriously affect the general conditions of the insects, only those experiments containing insects from the same culture can be considered to be strictly comparable. Care was taken to share the insects from a breeding culture between experiments so that each experimental batch was similar. The results for groups of experiments with insects of similar origins are placed together in the Tables.

In all experiments any developmental stage of the insect was considered to have survived if it could develop to the next active stage, namely an egg if it hatched and a larva or pupa if it became adult. Thus a larva referred to as dead may have died while still a larva or in the pupal state. An adult moth was considered to have survived if it could move at favourable temperatures (above 15°C.).

Experiments at constant Temperatures.

Apparatus and technique.

Temperatures below 1°C. were obtained in the ice box of a refrigerator in which an approximate relative humidity of 70 per cent. was maintained by a saturated aqueous solution of ammonium nitrate (Washburn, 1928), which also acted as an antifreeze solution. The temperature fluctuated cyclically with a range which varied between different experiments from ±0·2° to ±1·8°C. of the mean. The full temperature cycle occupied from 13 to 36 minutes. All mean temperatures given in Tables I to V are the means of the midpoints between the

TABLE I.

The effect of low temperature on the hatching of eggs at 70 per cent. R.H.

Expt. A	Exposure (days)	Temp. (°C.)		Stock I		Stock II		Stock III	
		Mean	Range	No.	% hatched	No.	% hatched	No.	% hatched
	1	−6·5	−5.5 to −7·0	5	0	17	0	17	0
	2	−6·5	−5·5 to −7·0	12	0	11	0	26	0
	7	−6·5	−5·5 to −7·0	7	0	20	5*	34	3*
	7	5·0	3·5 to 6·5	12	0	32	91	26	0
	14	5·0	3·5 to 6·5	12	0	25	4	30	0
	28	5·0	3·5 to 8·5	12	0	22	0	22	0
	Control	25·0	24·5 to 25·5	7	57	30	67	21	57
Expt. B	1	0·3	1·4 to −0·7	27	7	19	21	27	0
	7	0·3	1·4 to −0·8	21	0	26	0	23	0
	7	6·0	5·0 to 6·0	18	17	18	22	22	5
	14	5·5	3·5 to 6·0	22	0	16	0	22	0
	21	5·5	3·0 to 7·5	20	0	26	0	20	0
	7	9·0	8·5 to 9·5	21	38	24	42	29	28
	14	9·0	8·0 to 10·0	19	0	21	0	26	0
	21	9·0	7·0 to 11·0	22	0	23	0	20	0
	Control	20·5	20·0 to 23·0	18	100	24	67	25	12

Expt. C	Exposure (days)	Temp. (°C.)		Stock IV		
		Mean	Range	No.	% hatched	Approximate incubation period
	7	approx. 10		18	6	(hatched at 25°C.)
	14	9·5	8·5 to 10·5	18	0	
	7	13·0	12·5 to 13·5	18	17	(hatched at 25°C.)
		13.0	12.5 to 13·5	18	33	15 days
		18·5	18·0 to 19·0	36	89	7 days
	Control	20·0	19·5 to 20·5	18	100	6 days
	Control	25·0	24·5 to 25·5	18	100	5 days

* These larvae were found dead and partly emerged from the egg shell. They were probably about to emerge when placed at −6·5°C.

daily maxima and minima. The ranges given are the maximum and minimum temperatures recorded during the whole exposure. Thermocouples used to measure the temperature in the ice box were accurate to ± 0·2°C.

Temperatures between 3° and 13°C. were maintained in refrigerators and higher temperatures in constant-temperature rooms or in incubators. The thermographs recording these temperatures were accurate to ± 0·5°C. A relative humidity of 70 per cent., accurate to ± 6 per cent. or better, was maintained in the constant-temperature rooms. In refrigerators and incubators, desiccators containing caustic potash of specific gravity 1·239 were used.

Eggs for experiments were laid at 20° or 25°C. over a period of three days by moths collected directly from ships or from cultures. The eggs exposed were, therefore, in various stages of development. Generally they were kept in 2 × 1 inch tubes at not more than 36 eggs per tube, but the small size of the ice box made it necessary to use 2 × $\frac{1}{2}$ inch tubes during exposure to 1°C. or below.

Unless otherwise stated, the large larvae used for experiments varied from about half grown (0·5 cm. long) to mature specimens still active after being taken from cocoons. The pupae used were of diverse ages. As far as possible insects were divided into experimental batches of similar age judged by the length of body for larvae and the degree of pigmentation for pupae. At 1°C. and below, groups of ten or fewer larvae, pupae or adult moths were kept in 2 × $\frac{1}{2}$ inch tubes during exposure, but were transferred to 3 × 1 inch tubes for incubation at a favourable temperature. Above 1°C., larvae and pupae were kept at a density of 20 insects or fewer per 1 lb. jam jar, with a depth of about two inches of the

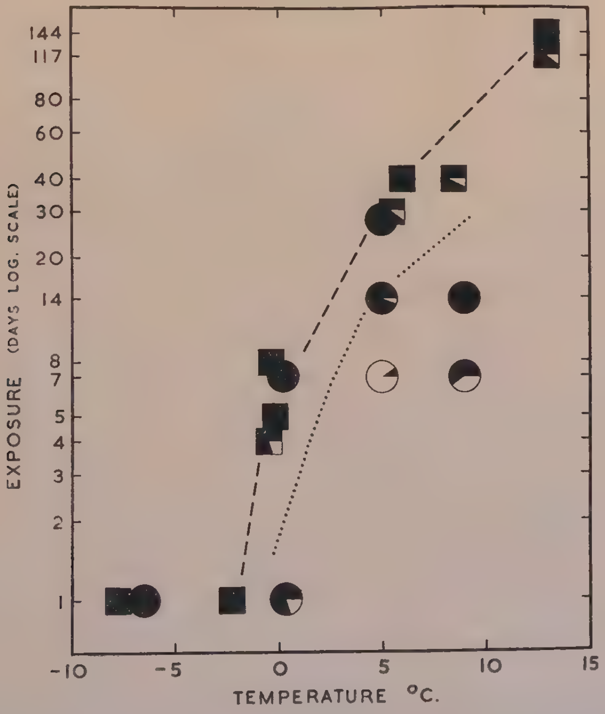


Fig. 1.—The percentage survival, shown by the white portion of each symbol, after various exposures to low temperature at approximately 70 per cent. R.H.

wheatfeed and glycerine mixture; adult moths do not feed and were kept without food.

After exposure to the experimental low temperatures the insects were frequently immobile. They were then incubated at 20° or 25°C. to test whether they were alive or dead. In experiments at 13°C. and below, the insects were kept at a temperature about half way between the experimental temperature and the breeding temperature for not more than one day before and after exposure. This reduced any lethal effects caused by a rapid temperature change, rather than by the exposure to cold. It also allowed some acclimatisation to moderately low temperatures, copying to some extent the conditions in storage places which usually involve temperature changes sufficiently slow to allow acclimatisation to occur. Acclimatisation is discussed on p. 833.

Results.

The results for each stage of the life-history are considered from three viewpoints, determination of the lowest temperatures at which the major changes in the life-cycle can occur, estimation of the shortest exposures to a number of low temperatures necessary to kill the various stages, and the effect of temperature on the time taken for development and on adult life and functions.

At the onset, it may be noted that there were some differences in survival at low temperatures between the batches of insects used. No one stock was consistently more resistant than the others and also, with any one stock, insects of different generations and from different cultures of the same generation showed

TABLE II.

The effect of low temperature on larvae.

Exposure (days)	Temp. (°C.)		Stock I				Stock II			
	Mean	Range	Larvae used	Died as larvae	Died as pupae	Adults	Larvae used	Died as larvae	Died as pupae	Adults
5	−0·2	−1·3 to 1·5	10	10	0	0	—	—	—	—
40	6·0	3·0 to 6·5	40	40	0	0	40	40	0	0
40	8·5	7·0 to 11·0	20	19	1	0	20	17	0	3
∞	9·5	7·0 to 11·0	20	19	1	0	20	18	2	0
41	13·0	12·5 to 13·5	20	6	0	14				
88	13·0	12·5 to 13·5	20	10	3	7	20	19	0	1
117	13·0	12·5 to 13·5	20	18	0	2				
∞	13·0	12·5 to 13·5	20	20	0	0	20	20	0	0
41	16·0	14·0 to 18·5	20	3	3	14				
68	15·5	14·0 to 18·5	20	10	2	8	20	13	0	7
117	15·5	14·0 to 18·5	20	2	13	5				
176	15·5	14·0 to 18·5	20	5	8	7	20	12	3	5
Control	20·0	19·5 to 20·5	40	11?	0	29	39	13?	0	26
Control	25·0	24·5 to 25·5	40	20?	0	20	40	18?	0	22

Larvae were taken from the same breeding cultures as were used to provide larvae for experiments referred to in Table VI and are comparable to them. The fate of some larvae, indicated by ?, is not certain as they were swamped by the next generation of larvae, but they did not become adult before the first adult of the next generation appeared.

large variations of survival. One of the most obvious inconsistencies is shown by eggs of stock II in Table I. Table IA shows a 91 per cent. hatch following seven days' exposure and a 4 per cent. hatch after 14 days' exposure at 5°C., whereas Table IB shows 22 and 0 per cent., respectively, for similar exposures at 5·5° to 6·0°C. of eggs of the same stock but of a different generation. A 67 per cent. hatch was obtained in the controls for both batches. As a result of such differences, only the most resistant batches and stocks are considered when assessing the shortest periods at low temperatures necessary to kill each developmental stage.

The *egg* hatched at temperatures between 13° and 35°C. but not at 9·5°C. (Tables IC & V). At 13° and 35°C. fewer eggs hatched than at less extreme temperatures. Yatomi & Yamashita (1938) state that eggs will hatch at temperatures between about 10° and 38°C.

The results of exposing eggs to temperatures below 10°C. are given in Table I and are summarised diagrammatically in fig. 1. The shortest exposures necessary to kill all eggs of all stocks are: less than one day at −6·5°C., about three days

TABLE III.

The effect of low temperature on large larvae at 70 per cent. R.H. No large differences occurred between the stocks which are grouped together.

Exposure (days)	Temp. (°C.)		Died as larvae	Died as pupae	Adults
	Mean	Range			
A.—Stock I					
1	−7·7	−7·5 to −8·0	10	0	0
2	−7·5	−6·5 to −8·0	10	0	0
3	−7·2	−6·5 to −8·0	10	0	0
4	5·0	3·5 to 6·5	2	0	8
14	6·0	3·5 to 8·5	3	0	7
30	5·5	3·5 to 8·5	9	0	1
Control	25	24·5 to 25·5	2	0	7
B.—Stocks II and III					
1	−2.3	−1·5 to −3·0	10	0	0
1	−2·6	−1·8 to −3·3	10	0	0
1	−3·1	−2·3 to −3·8	10	0	0
Control	25	24·5 to 25·5	3	4	3
C.—Stocks I, II, III and IV					
1	−0·7	−0·3 to −1·2	13	2	8
2	0·1	0·6 to −1·2	11	1	6
4	−0·5	0·5 to −1·3	18	0	1
8	−0·4	0·5 to −1·3	20	0	0

at 0·3°C. and about 20 days at 5°C. as shown by the dotted line in fig. 1. All the eggs exposed for 14 days at 9° and 9·5°C. were killed, but one survived after 14 days at 5°C. Therefore a much longer period than this at 10°C. is necessary to be sure of killing all eggs.

Fukaya (1939) obtained an incubation period of four days at 24°C. The approximate figures of five days at 25°C. and of six days at 20°C. given in Table IC agree quite well with this.

The effects of *low temperature on large larvae* are shown by the results of experiments given in Tables II, III and IV. In the three experiments left at 15°C. for as long as 12 weeks, nine larvae became adult while still at 15°C. and eight did so during incubation at 25·5°C. At 13°C., however, no larvae pupated, although some were still alive after exposure for 117 days at this temperature, two becoming adult late during incubation (Table II). Thus the lowest temperature at which large larvae can complete their life-cycle is between 13° and 15°C. The lowest temperature at which a larva pupated was 8·5°C. (Table II).

TABLE IV.

The effect of low temperature on large larvae, pupae and adults of stock IV.

	Temp. (°C.)		Larvae			Pupae		Adults
Exposure	Mean	Range	Died as larvae	Died as pupae	Adults	Died as pupae	Adults	No. alive two days after exposure
8 hours	−1·4	−0·9 to −2·2	4	3	1	0	8	4 out of 5
1 day	,,	,,	7	1	0	2	6	4 ,, ,, 5
3 ,,	,,	,,	7	1	0	4	4	0 ,, ,, 5
5 ,,	,,	,,	7	1	0	8	0	0 ,, ,, 5
7 ,,	,,	,,	7	1	0	8	0	0 ,, ,, 5
9 ,,	,,	,,	8	0	0	8	0	0 ,, ,, 5
Control	20	19·5 to 20·5	4	0	8	3	12	17 out of 20
Continuous	4·0	0 to 7	24	0	0	24	0	
,,	9·5	8·3 to 11·5	24	0	0	24	0	
,,	13·0	12·5 to 13·5	22	2	0	16	8	
Control	20·0	19·5 to 20·5	3	1	8	3	12	

At −1·4°C. or below all the larvae exposed for one day were killed, but one survived after exposure at −1·4°C. for eight hours (Tables III and IV). One larva survived exposure for four days at −0·5°C., but all the larvae exposed for eight days at −0·4°C. were killed (Table IIIC). All the larvae exposed for 40 days at 6°C. died (Table II), but one larva became adult following exposure for 30 days at 5·5°C. (Table IIIA).

The results of experiments in which the larvae were most resistant to cold are collected together in fig. 1. On this figure the broken line gives an estimate of the shortest exposures to low temperatures necessary to kill all larvae. These include 1 day at −1°C., 5 days at 0°C., 32 days at 5°C. and 83 days at 10°C.

Pupae can become adult at 13°C. but not at 9·5°C. (Tables II & IV). All the pupae exposed for five days at −1·4°C. died, but four became adult after exposure for three days.

The *complete developmental cycle* (egg laid to adult) on wheatfeed in small cultures takes about 64 days at 20°C. (humidity varying between 50 and 70% R.H.) and about 41 to 45 days at 25°C. (70% R.H.).

Adult moths live longest (14 to 18 days) at the comparatively low temperature of 9° to 10°C. This is shown by fig. 2. The circles give approximate mean values for the length of adult life. These values were obtained from experiments in which moths, first exposed when less than one day old, were examined at room temperatures at intervals of three to four days to decide whether they were still alive. Each dead moth was discarded after sexing and was assumed to have died half way through the preceding interval. In another set of experiments (crosses in fig. 2), adults of mixed age were used and examined daily. These moths were assumed to have passed, on average, half their lives before the experiment began, so the mean periods of life recorded have been doubled.

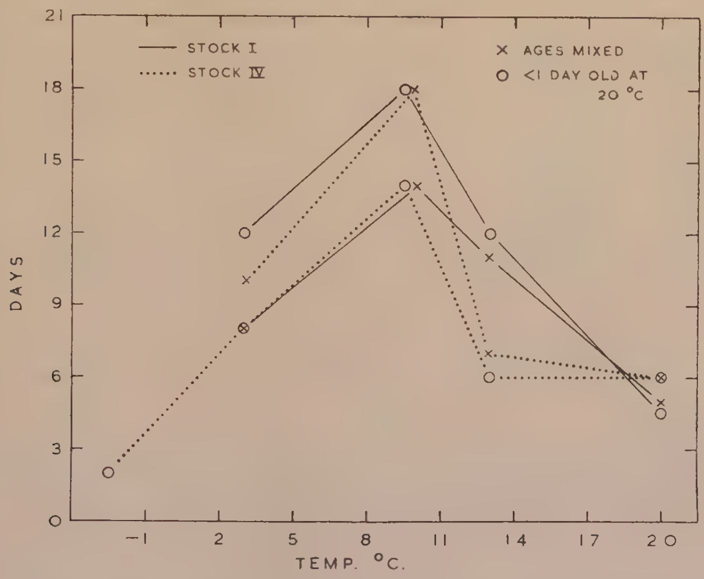


Fig. 2.—The mean length of life of adult moths at low temperatures.

Between 8 and 29 moths were used for each experiment except that at 9·5°C. with young adults for which one moth only was used.

At temperatures below 9°C. adult life is shortened by cold. At 3°C. they lived for a mean of 8 to 12 days. Adults were alive, *i.e.*, they could still move when returned to 20°C. after an exposure of one day at −1·4°C., but they were killed by an exposure of three days (Table IV).

Adult life becomes shorter as the temperature rises above 10°C., probably as a result of quicker metabolism. At 20°C. adults lived less than half as long as at 10°C. (fig. 2). Adults of the insectary stock lived two to three days longer at 20°C. than at 25° to 33°C., but at 25°, 30° and 33°C. there was no appreciable difference in the length of life (Table V). At 35°C. adults lived only 3·6 days.

Comparing the length of adult life at temperatures above and below the optimum for long life, the moths used for the experiments shown in fig. 2 lived longer at 3°C. than at 20°C. As might be expected, exposure of moths of stock IV to temperatures between 3° and 13°C. for a few days followed by return to 20°C. caused a slight lengthening of the total adult life compared with moths kept continuously at 20°C. The exposures used were:—

TABLE V.

The effect of temperature at 70 per cent. R.H. on adult life and egg-production of an insectary stock.

Temp. (°C.)		Moths used	Adult life (days) M ± S.E.	Eggs per female	% hatched
Mean	Range				
35°	34·5 to 35·5	7	3·6 ± 0·3	28	1
33°	32·5 to 33·5	11	5·6 ± 0·4	43	10
30°	29·5 to 30·5	11	5·5 ± 0·4	59	5
25°	24·5 to 25·5	11	5·8 ± 0·3	45	15
20°	19·5 to 20·5	17	8·4 ± 0·5	65	24
13°	12·5 to 13·5	25	12·6 ± 0·9	26	2
5°	7·0 to 4·0	15	7·6 ± 0·3	0	

4 days at 3·5°C. (range 3·0° to 4·0°)
5 ,, ,, 9·0°C. (,, 8·5° to 11·0°)
5 ,, ,, 13·0°C. (,, 12·5° to 13·5°)

The length of adult life of moths of the insectary stock (Table V) was longer at 20°C., but shorter at 5°C. than that of moths of stocks I and IV at similar temperatures (fig. 2). This decreased tolerance of cold by insectary moths may be due to long conditioning to continuously favourable temperatures by prolonged culture in the insectaries.

The longest adult life recorded for individual moths from all the stocks used at various temperatures was: 16 days at 3°C., 28 days at 10°C., 21 days at 13°C., and 13 days at 20°C.

An analysis of variance of results shown in Table V showed that differences in the length of life of moths of the two sexes were not significant.

Moths kept at 13°C. and below are very lethargic and, therefore, they probably copulate infrequently or not at all in these conditions. This contention is supported by the results of examination of the bursa copulatrix of 77 females of mixed ages. These moths had been removed from 20°C. and kept at constant temperatures between 5° and 13°C. until they died. No spermatophores were found in 19 moths which presumably had been virgin on transfer to low temperatures and were prevented by cold from mating.

Only small numbers of eggs were laid at temperatures of 13°C. and below, either by adults of stock VI, or by adults in the experiments illustrated in fig. 2, or by adults of stock IV during their exposure for 4 or 5 days at temperatures between 3° and 13°C. referred to above. However, adults of an insectary stock laid 26 eggs per female at 13°C., which is about half the numbers laid by the same stock at temperatures between 20° and 33°C. (Table V).

Exposure of moths of stock IV to temperatures between 3° and 13°C. (above) did not impair subsequent egg-production at 20°C. However, the fertility of the eggs produced was reduced, 88 to 57 per cent. of eggs laid at 20°C. by these adults being infertile compared with the 28 per cent. infertile eggs laid by moths kept continuously at 20°C. A few infertile eggs were laid at a favourable temperature by a virgin moth after exposure for eight hours at −1·4°C.

At 35°C., moths of the insectary stock laid fewer eggs than at temperatures between 33° and 20°C. (Table V). Norris (1934) obtained fewer eggs at 18° to 20°C. (104 eggs per female) than at 27°C. (five batches with means of 160 to 282 eggs per female). This level of egg-production is two to four times as great as that obtained from the insectary stock (Table V).

The lowest temperatures at which the major changes in the development cycle can take place are: hatching, between 10° and 13°C.; pupation, 8·5°C. and the change to adult, between 10° and 13°C.

When comparing the resistance to cold of the *various stages in the life-cycle*, the differences between the criteria used for the survival of each stage must be borne in mind. For instance, for adult moths their ability to move following an exposure to low temperature has been used. If this was also used for larvae instead of survival to become adult, then larvae would appear to be much more resistant to cold. Using the criteria set out on p. 814, the shortest periods, in days, at low temperatures in which all the individuals of the various stages die are:—

	Egg	Large larva	Pupa	Adult
−1°C.	—	1	3 to 5	1 to 3
0°C.	about 3	5	—	4 to 5
5°C.	about 20	about 32	—	17

Pupae were more resistant to low temperatures than large larvae which in turn were more resistant than eggs. Adults were less resistant to a rapidly lethal low temperature (−1°C.) than pupae, but more so than large larvae.

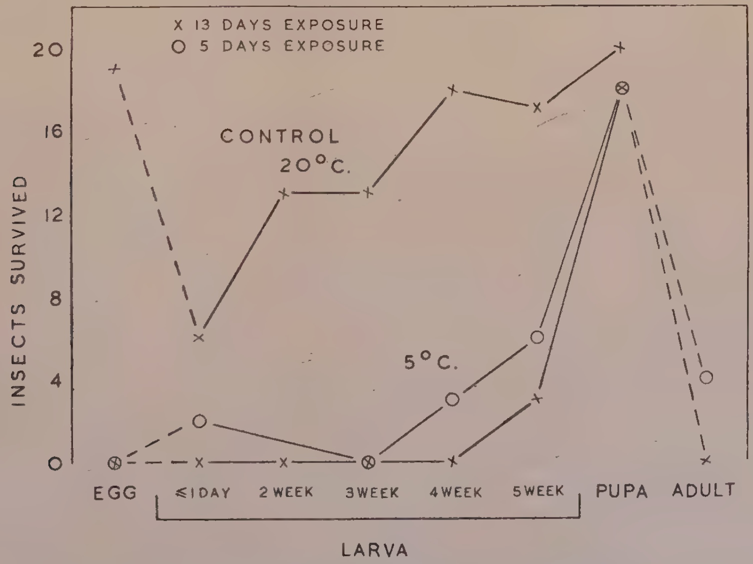


Fig. 3.—Survival of different stages of stock V after exposure to 5°C., 70 per cent. R.H., using 20 insects for each test.

An experiment designed to compare the resistance of the various stages of the same stock under conditions that were as far as possible identical is illustrated in fig. 3. The mean temperatures experienced by the various stages varied from 4·5° to 5·2°C. This experiment confirms the statement made above concerning the relative resistance to cold of eggs, large larvae and pupae. In addition, it shows that large larvae, five weeks old at 20°C., were more resistant than the younger larvae. Four adults were alive after five days' exposure at 5°C., but all were dead after 12 days' exposure. The adults kept at 20°C. lived a mean of 3·7 days.

Experiments at variable Temperatures.

Method and conditions.

Larvae of all the stocks available were placed in three outbuildings and a screen during the winters of 1949–50 and 1950–51 to determine directly the effects of the English winter.

The most exposed site was the screen, which was 18 by 8 in. internal dimensions, 18 in. from the ground, 15 yd. to the west of the laboratory and slightly shadowed by it. Two of the outbuildings were unheated. One was a large prefabricated hut (Building 1) with inner walls of celotex and outer walls of roofing felt separated by an air space. The roof was made of the same materials without an air space and with no ceiling. The floor was cemented. The other was a small summer-house (Building 2) with a ceiling of metal sheeting, wooden walls lined with similar metal sheeting and with a cement floor. The third outbuilding was a small all-wooden hut (Building 3) 9 × 14 ft. with no ceiling. This was heated during the day-time on most working days by an electric fire. The day-time heat soon dissipated and had little effect on the minimum night temperatures.

The larvae were kept in 1 lb. jam jars on the floor in Building 2, and on the floor of a metal bin, six ft. cube, in Building 1. In Building 3, one set was kept on the bench and another set on the floor in a small cardboard box lagged with two to three in. of cotton waste.

A recording thermograph, giving records accurate to ±1°C., was kept in each position. Each instrument was checked at intervals against a thermometer. The daily maximum and minimum temperatures and the number of hours at each temperature were obtained from the thermograph charts. The daily minimum usually occurred in the early morning and the maximum in the afternoon. This diurnal rhythm was borne in mind when obtaining the daily maximum and minimum temperatures, so that the period midnight to midnight was not always strictly adhered to. For instance, when the temperature just before midnight was lower than the minimum for the following morning, it was used in place of this minimum for the day in question. Occasional gaps in a record due to a clock stopping or a pen failing were filled in by comparison with the records for the other sites. No humidity low enough to have any effect on the larvae was recorded.

During 1949–50, larvae of stocks I, II and III were used. The initial breeding culture of each stock had been divided up into a number of subcultures to reduce crowding. On 6th October 1949, larvae were removed from several subcultures and the larvae from each were divided into groups of equal size. Batches of 20 larvae with a similar breeding history were formed by combining one group from each subculture. In this manner, 24 batches were made up from stock I, 15 from stock II and 3 from stock III. Each batch was placed on 2 in. of wheatfeed plus 5 per cent. glycerine in 1 lb. jam jars. The jars were distributed between the various exposure sites as shown in Table VI and between the two constant temperatures 20° and 25°C. shown in Table II, which served as control temperatures for these experiments. The jars of larvae at 20° and 25°C.

TABLE VI.

Resistance of larvae to variable temperatures during the winter of 1949–50.

Situation	Exposure dates	Exposure (days)	Sums (see text)	Stock I		Stock II		Stock III		Stock I "mixed cultures"	
				Alive when placed at 25°C.	Adults	Alive when placed at 25°C.	Adults	Alive when placed at 25°C.	Adults	Alive on 31.iii.	Became adult after 31.iii. at variable conditions
Building 1	6.x. to 16.xi.	41	8	—	12	—	—	—	—		
	6.x. to 13.xii.	68	18	3P, 12L	14	—	—	—	—		
	6.x. to 31.i.	117	45	16L	8	9L	2	—	—		
	6.x. to 31.iii.	176	76	10L	1	11L	2	9L	1		
	19.x. to 31.i.	104	45	—	—	—	—	11L	0		
	19.x. to 31.iii.	163	76	—	—	10L	2	2L	0	70L	0
Building 2	6.x. to 16.xi.	41	10	—	16	—	—	—	—		
	6.x. to 13.xii.	68	24	2P, 13L	9	—	—	—	—		
	6.x. to 31.i.	117	85	13L	9	8L	1	—	—		
	6.x. to 31.iii.	176	119	0	0	2L	0	1L	0		
	19.x. to 31.i.	104	85	—	—	—	—	0	0		
	19.x. to 31.iii.	163	119	—	—	2L	0	0	0	5L	0
Building 3	19.x. to 16.xi.	28	—	—	19	—	—	—	—		
	19.x. to 13.xii.	55	—	19L	10	—	—	—	—		
(box)	19.x. to 31.i.	104	—	9L	8	—	—	—	—		
	19.x. to 31.iii.	163	—	9L	2	12L	1	0	0	53L	4
Building 3	19.x. to 16.xi.	28	—	—	17	—	—	—	—		
	19.x. to 13.xii.	55	—	19L	13	—	—	—	—		
(bench)	19.x. to 31.i.	104	—	13L	7	—	—	—	—		
	19.x. to 31.iii.	163	—	13L	2	10L	0	0	0	129L	approx. 10
Screen	19.x. to 31.iii.	163	306	3L	0	1L	0	—	—	16L	0
Controls	at 20° and 25°C.		—	80L	49	79L	48	20L	13	Formed dense cultures	

All cultures, other than the " mixed cultures ", were started with 20 larvae and incubated at 25°C., 70% R.H. after exposure. L = larva; P = pupa.

also acted as controls for an additional 20 batches of 20 larvae set up on the 19th October in the same way and from the same breeding subcultures as shown in Table VI.

The food in the control jars was tipped out approximately weekly and the insects counted. Caterpillars of the second generation may have killed some of the original larvae which were still in the larval stage, consequently the death rate recorded in these controls may be too high.

The experimental insects were removed on one of four dates (see Table VI) from the exposure sites and incubated at 25°C. Superficial examinations were made weekly during exposure. On removal for incubation, the food was tipped out and the insects still alive were counted. The insects were counted weekly during incubation.

The technique was modified slightly during 1950–51. Stock IV was included and larvae from six breeding cultures were used, controls being set up for every breeding culture. As soon as some adults appeared, the remaining larvae were placed on fresh food so that they would not come into contact with the second generation. During exposure, the insects were counted approximately monthly and superficial examinations were made weekly. In 1949–50, the last insects were removed for incubation on 31st March and were not exposed to the spring

TABLE VII.

Resistance of larvae and pupae to variable temperatures during the winter of 1950–51.

Situation	Stock	Exposed on	Insects used	Adults produced	Larvae alive on			Last death
					1.i.	21.ii.	4.iv.	
Control 20°C.	I	15.xi.	20L	16				
	II	6.x.	18L 3P	13				
	III	10.x.	9L	8				
	IIIA	10.x.	11P	8				
	IVA	10.x.	19L	12				
	IVB	8.xi.	20L	17				
	IVC	1.ii.	20L 60P	69				
Building 1	I	15.xi.	20L	0	2	—	—	To 20°C., 1.i.
	I	15.xi.	40L	0	2	0	0	Feb.
	II	6.x.	19L	0	4	0	0	Feb.
	III	10.x.	9L	1 in Dec.	5	2	2	April
	IVA	10.x.	11P	2 in Oct.	—	—	—	To 20°C., 4.iv.
	IVA	10.x.	20L	0	13	8	1	June
	IVB	8.xi.	20L	0	3	—	—	To 20°C., 1.i.
	IVB	8.xi.	40L	0	1	0	0	Feb.
	IVC	1.ii.	20L 60P	0	—	11	6	April
Building 2	I	15.x.	20L	0	2	—	—	To 20°C., 1.i.
	I	15.xi.	40L	0	0	0	0	Late Dec.
	IVB	8.xi.	60L	0	2	0	0	Feb.
	IVC	1.ii.	40L 120P	0	—	10	0	March
Screen	I	15.xi.	60L	0	0	0	0	Dec.
	II	6.x.	19L 3P	0	0	0	0	Dec.
	III	10.x.	9L	0	7	0	0	Feb.
	IVA	10.x.	11P	1 in Oct.	—	—	—	Doubtful
	IVA	10.x.	20L	0	0	0	0	Dec.
	IVB	8.xi.	60L	0	0	0	0	Dec.
	IVC	1.ii.	40L 120P	0	—	9	3	April

All controls produced good second generations. L = larva; P = pupa.

weather which was quite cold. In 1950–51, however, some insects were exposed until June to determine the number actually surviving into the summer. An additional batch of insects was first exposed in February to discover whether midwinter immigrants could survive the latter part of the winter. During this second winter some pupae were included in the experiment.

The overwintering stage of development.

During 1949–50, cultures containing some insects at all stages of development, including eggs and adults, were exposed alongside jars of the principal experiments which contained only larvae. In Table VI these are referred to as mixed cultures. They produced similar results to the principal experiments, there being no indication that any stage is more likely to survive the whole winter than the large larvae.

In all experiments very few larvae and pupae became adult while exposed to winter conditions. Only one larva did so out of a total of 976 larvae exposed at the four sites until January in both winters. No adults were obtained from the batch of 100 larvae which was exposed from February 1951. Adults were obtained during October from 3 out of 25 pupae which were exposed from early October 1950, but none of the 300 pupae exposed from February 1951 became adult (Table VII). All the adults produced died in the early winter.

A comparison of the winters of 1949–50 and 1950–51.

Better survival was obtained after the winter of 1949–50 than after that of 1950–51. Out of 360 larvae exposed from October 1949 until the end of March 1950, 95 were still alive on 31st March 1950. Eleven of these became adult after removal to 25°C. (Table VI). During 1950–51, however, only three of the 396 larvae exposed from October and nine of the 100 larvae exposed from February were still alive at the end of March and these died later while exposed to the fairly cold weather of spring.

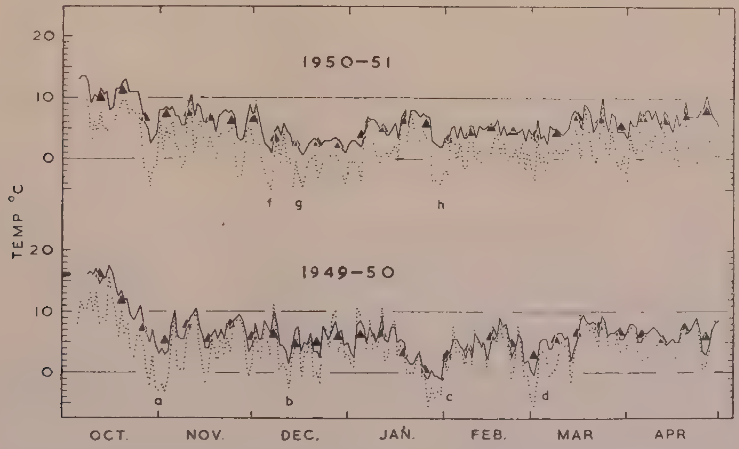


Fig. 4.—Daily minimum temperatures in Building 2 (complete line) and in the screen (dotted line). Mean weekly minima in Building 2 are shown by triangles and a to h mark some cold spells.

The lower survival after the winter of 1950–51 is due mainly to the greater severity of this winter, which is illustrated by minimum temperatures given in fig. 4. In the screen from October 1950 until the end of March 1951, the temperature fell below $-0{\cdot}5$°C. for 402 hours as against only 167 hours for the comparable period of 1949–50. Also, the minimum temperature fell below zero on 59 days in 1950–51 compared with only 27 days in 1949–50.

A better comparison of the lethal effects of weather conditions is obtained by taking into account not only very low temperatures, which kill the larvae rapidly, but also those at which they die very slowly. A mortality index based on the data for constant temperature has been devised for this purpose.

The index given to each temperature at degree intervals up to 10°C. is obtained by taking for each temperature the reciprocal of the shortest exposure in days required to kill all the larvae used (fig. 1). The indices are as follows:—

°C.	Shortest lethal exposure (days)	Index
< −0·5°	1	1·000
−0·5° to 0·5°	5	0·200
0·5° to 1·5° ..	8	0·125
1·5° to 2·5° ..	11	0·091
2·5° to 3·5° ..	16	0·062
3·5° to 4·5° ..	23	0·043
4·5° to 5·5° ..	32	0·031
5·5° to 6·5° ..	40	0·025
6·5° to 7·5° ..	47	0·021
7·5° to 8·5° ..	58	0·017
8·5° to 9·5° ..	70	0·014
9·5° to 10·5° ..	83	0·012

If the shortest lethal exposure for any constant temperature is multiplied by its mortality index, a standard product of one day-unit is obtained which is the minimum product required to give a complete kill.

This was applied to variable conditions using the thermograph records. With these records it was more convenient to work in hours, so that the product of the index and the exposure in hours for complete kill would be 24 hour-units for each of the constant temperatures listed above.

The number of hours recorded each day at each of the above temperatures was estimated from the thermograph record. Every day the period obtained at each temperature was multiplied by the appropriate index.

The sum of the values for each day was found as shown in the following example for Building 2 on 4th November 1949:—

Hours	Temp. °C.	Mortality index	Product (hour-units)
5 ..	7·5° to 8·5°	0·017	0·085
8 ..	8·5° to 9·5°	0·014	0·112
1 ..	9·5° to 10·5°	0·012	0·012
10 ..	>10·5	0	0
			Sum 0·209

If, at variable temperatures, larvae die at the same rate as they do in similar constant low temperatures and show no recovery at all when the temperature increases to become no longer harmful, then a complete kill should be obtained when the sum of mortality index products reaches 24 hour-units. No allowance is made for recovery during periods of favourable temperature. However, some recovery must take place, since the smallest sums which proved necessary to kill all the larvae exposed from October are about 100 units. This is shown by fig. 5, in which the survival of insects at the exposure sites is plotted against the mortality index sums obtained. Although they failed to become adult when incubated, some larvae were still alive in the screen in March 1950, after an exposure equivalent to 306 units. The 20 larvae which were first exposed in Building 1 on the 1st February 1951 all died, the sum being only 35. This comparatively rapid mortality may have been due to shock caused by the sudden removal of the insects from the breeding temperature of 20°C. to 4°C. occurring in Building 1.

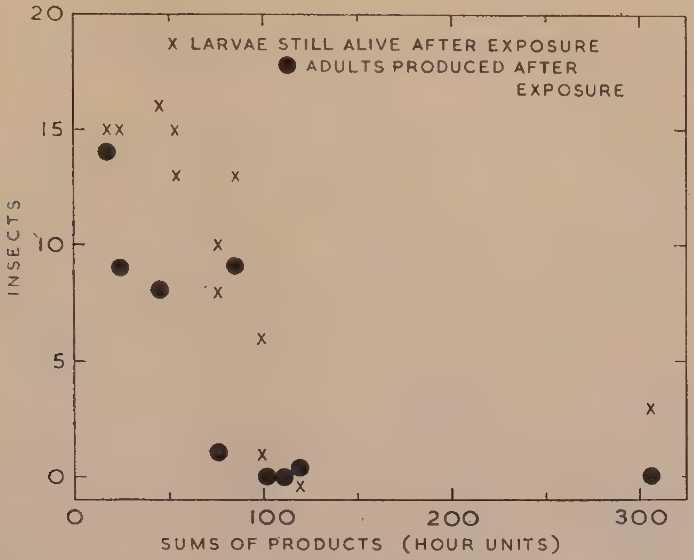


Fig. 5.—Survival of groups of 20 larvae of the most resistant strains used in both winters plotted against the sums of the mortality index products calculated for the periods at the exposure sites.

The greater lethal power of the weather conditions during 1950–51 can be shown by comparing the sums of the mortality index products obtained for one of the exposure sites. For Building 1, the sum up to the end of March was 76 units for 1949–50 and 97 units for 1950–51. This higher sum was obtained in spite of the bin containing the experiments in this building being covered by a sheet of asbestos in 1950–51, so that in fact no temperatures below 2°C. were recorded during this year, although in 1949–50 the minimum temperature fell below zero on two days.

As it is very laborious to obtain the number of hours at each temperature and to calculate the mortality index sums, six easier methods of comparison were tried in the hope of finding one particularly suitable for *E. cautella*.

These six methods (Table VIII), all of which are based on the daily minimum temperatures, are:— (A.) the coldest monthly mean of the daily minima, (B.) the average of the three coldest monthly means of daily minima; both of these were selected as measures of the coldest part of the winter, (C.) the number of weekly mean minima below 5°C.; this includes the short cold periods during the whole exposure, (D., E. and F.) the numbers of daily minima below 0°, 2° and 5°C., which give the number of cold days. These three temperature limits were selected as being quickly lethal (fig. 1) and also of reasonably frequent occurrence at some at least of the sites.

From left to right in Table VIII, the exposure sites are arranged in approximate order of severity as judged by the survival of the insects. The sites fall into three divisions:— (1) No live larvae present at the end of March; (2) Some live larvae found at the end of March none of which survived to become adult; (3) Survival.

TABLE VIII.

A comparison by six methods of the winter temperatures experienced by the insects at three exposure sites.

	Division 1	Division 2				Division 3
	Screen, 1950–51 (Oct. to 14th Feb.)	Screen, 1949–50 (Oct. to March)	Building 2, 1950–51 (Oct. to 14th Feb.)	Building 2, 1949–50 (Oct. to March)	Building 1, 1950–51 (Oct. to March)	Building 1, 1949–50 (Oct. to March)
Sum of products ..	—	306	—	119	97	76
A. Coldest monthly mean minimum, °C.	0·7	2·8	3·3	3·9	4·9	5·5
B. Average of the three coldest monthly mean minima, °C.	0·6	3·5	4·3	4·8	5·2	6·2
C. Weekly mean minima equal to or below 5°C.	17	10	7	7	7	2
D. Daily minima equal to or below 5°C. ..	178	118	59 (93*)	85	61	47
E. Daily minima equal to or below 2°C. ..	74	61	20 (21*)	27	4	7
F. Daily minima equal to or below zero ..	59	40	1	8	0	2

* October 1950 to March 1951.

Building 2 for 1950–51 is included in Division 2, in spite of the absence of live larvae at the end of March, because larvae from the two stock cultures which provided the most cold-hardy insects during this winter were not included at this site.

The methods of comparing temperatures which agree best with this division of the exposure sites should be the best measures of severity for use in relation to *E. cautella*. There is a sharp difference between Divisions 1 and 2 in the three lots of mean minimum temperatures and in the number of daily minima below 5°C. However, the numbers of daily minima below 2° and 0°C. in the screen for 1949–50 are nearer to the numbers for the screen in 1950–51 than to those for the other sites placed in Division 2. These two criteria also fail to distinguish between Divisions 2 and 3, although the other four criteria show Division 3 to be clearly the warmest. In addition, these two criteria are frequently not representative of the severity of the whole winter. For instance, all the seven minima below 2°C. in Building 1 (1949–50) occurred during two cold spells, one at the end of January and the other at the beginning of March. There is considerable variation in severity between the sites in Division 2. Most variation is shown by the numbers of daily minima below 2°C. and below 0°C. and least by the number of weekly minima below 5°C. (Table VIII).

The number of daily minima below 2°C. and below 0°C. are quite obviously inadequate criteria. The number of daily minima below 5°C. and the three criteria using means of daily minima are reasonable. Since it involves no division into arbitrary periods of time, namely weeks or months, the use of the number of daily minima below 5°C. is to be preferred.

A comparison of four winters.

Mansbridge (1936) exposed cultures of *E. cautella* in a small unheated building at the laboratory in Slough during two winters, 1934–35 and 1935–36, so that information about overwintering in a total of four winters is available.

The severity of these winters can be judged by comparing the monthly means of the daily minimum temperatures for Kew Observatory, about 13 miles from Slough. These are published in the Monthly Weather Reports (Meteorological Office, 1934–52):—

Period	Monthly mean of the daily minimum temperatures (°C.)	
	Coldest month	Average of 3 coldest months
1934–35	3·4°	4·0°
1949–50	2·8°	3·3°
1935–36	1·0°	2·2°
1950–51	0·6°	1·8°
1934–35 to 1952–53 inclusive, warmest	3·4°	4·0°
,, ,, average	1·2°	2·3°
,, ,, coldest	2·2°	0·2°

The winter of 1934–35 was the warmest winter during the last 18 years, 1949–50 was warm, 1935–36 was very slightly colder than average and 1950–51 was the sixth coldest winter. This period of 18 years was slightly warmer than the 35 years 1881 to 1916 given by Bilham (1938). The averages of the monthly means of the daily minimum temperatures for the winter months November to March are 3·4° and 2·3°C. for the two periods, respectively.

The site used by Mansbridge was a small unheated brick building which compares best with Building 2. He published the absolute monthly minima for the two winters. By adding the difference between these minima and corresponding values for Kew to the monthly means of the daily minima for Kew, estimates of the monthly means of the daily minima for Mansbridge's building were obtained.

The average of the monthly means of the daily minima for the months October to March was 3·1°C. higher for Mansbridge's building than for Kew in 1934–35 and 3·3°C. higher in 1935–36. A similar comparison between Building 2 and Kew gives differences of 1·5°C. for 1949–50 and 2·5°C. for 1950–51. Thus, Building 2 was influenced by the winter weather slightly more than the building used by Mansbridge. The available methods of comparing the temperatures in the two buildings are rather limited. Four methods, two of which are derived from Table VIII (B and F), and two of which involve the *absolute* minima of weekly periods, are given below:—

Winter	Average of the monthly means of the daily minima for the coldest 3 months (B of Table VIII) (°C.)	Period 18th Nov. to 30th Apr.		
		No. of weekly absolute minima below		No. of days below zero (F of Table VIII)
		5°C.	2°C.	
1934–35	7·1° estimated	16	5	0
1935–36	5·5° estimated	21	13	11
1949–50	4·8°	18	5	8
1950–51	4·3°	21	6	1

Some insects survived 1934–35, which is shown by all four methods of comparison to be the warmest winter.

No insects survived the winter of 1935–36 or that of 1949–50. In 1935–36 all the larvae used were dead by February and in 1949–50 five were still alive at the end of March, but there was little difference between the conditions inside the two buildings.

No survival occurred after the winter of 1950–51, all the larvae being dead by February. The mean minima of the three coldest months show this to be the coldest winter, although there were fewer very cold daily and weekly minima than in some of the earlier winters.

The death of all the larvae in Building 2 by February 1951 may have been due to the coldest month of the winter occurring as early as December 1950. However, also in 1935–36 all the larvae were dead by February, which itself was the coldest month.

The effect of cold spells.

The cumulative effect of the various cold spells in 1949–50 was tested by removing replicate jars from the three buildings for incubation after each cold spell. This was necessary because it is very difficult to decide when a larva kept at low temperatures is dying.

Noticeable cold spells in 1949–50 are marked a, b, c and d in fig. 4. Not one of these was severe enough to kill all the larvae used, as some survived in every batch of replicate jars removed from Buildings 1 and 3. However, each cold spell probably killed some larvae, as Table VI shows a progressive decrease in the number of larvae still capable of becoming adult in replicates removed after each successive cold spell. No cold spell produced any single exposure in the buildings comparable in severity to those which were completely lethal at constant conditions. However, no adults were produced by the larvae from the replicates removed from Building 2 on 31st March 1950, one month after the last cold spell, but as these larvae were exposed to the whole winter this latest cold spell cannot be regarded as being the chief cause of the complete kill.

In 1949–50, there was no continuous period of 24 hours or more in the screen at −1°C. or below, which is necessary at constant temperature for a complete kill. In 1950–51, such periods occurred on three occasions marked f, g and h in fig. 4. At the beginning of January, after experiencing two of the cold spells, some larvae were still alive in the screen, but they were dead in February after the third cold spell. As no replicates were removed from the screen for incubation, it is not known definitely whether the early cold spells would have prevented larvae becoming adult, but they should have done so, as no larvae survived in replicates removed from Building 1 on 1st February 1951, even though the lowest temperature recorded in this building was only 2°C.

The effect of winter conditions on the different stocks.

Table VI shows that the three stocks used in 1949–50 all exhibited similar levels of mortality in control conditions (35 to 40% died), but they differed considerably in their resistance to cold. By combining the results of experiments shown in Table VI in which the length of exposure was similar (Table IX), it can be seen that stock I was more resistant to this winter than stock II, which in turn was more resistant than stock III. There is a slight exception in that 44 per cent. of the 80 larvae of stock II exposed in Buildings 1, 2 and 3 were still alive 3rd March 1950, compared with 40 per cent. of the larvae of stock I: on the other hand only four per cent. of the larvae of stock II became adult compared with six per cent. of the larvae of stock I (Table IX). G. A. Brett (unpublished) obtained a similar relationship for the resistance of stocks I, II and III in his warehouse experiments.

TABLE IX.

Survival of larvae exposed from October 1949.

Stock	40 larvae exposed until 31.i.50 in Buildings 1 and 2		80 larvae exposed until 31.iii.50 in Buildings 1, 2 and 3	
	Larvae alive on 31.i.50	Adults	Larvae alive on 31.iii.50	Adults
I	29=72%	17=42%	32=40%	5=6%
II	17=42%	3= 7%	35=44%	3=4%
III	11=27%	0= 0%	10=12%	1=1%

Control mortality for these three stocks during 1950–51 was more variable, the percentages being 20, 40 and 11, respectively. This suggests that stock III was in better condition in this year than stocks I and II. This is also reflected in the greater resistance to cold shown by stock III (Table VII), which was the least resistant stock in 1949–50. Two cultures (A and B) of stock IV were also used, the mortality in the controls being A, 37 per cent. and B, 15 per cent. In Building 1 insects from culture A, however, proved to be more resistant to cold than those from culture B. Shock on the first day of exposure may have contributed to the poorer resistance of insects from culture B, as the minimum temperature on the first night was 4°C. for B compared with only 9°C. for A.

The differences in the comparative resistance of stocks I, II and III in the two winters, and the difference in resistance of insects from two cultures of the same stock, suggest that factors arising in culture have caused these differences rather than any inherited factor of the stock.

Discussion.

Four species of the subfamily Phycitinae are common in warehouses in Britain, *Ephestia cautella*, *E. elutella* (Hb.), *E. kuehniella* Zell., and *Plodia interpunctella* (Hb.). Of these, *E. cautella* is the least resistant to cold (Mansbridge, 1936).

The severity of the winter determines the number of *E. cautella* surviving in jam jars in small buildings of the type used in the present work. Some larvae survived the mild winters of 1934–35 and 1949–50, but none survived until the summer through the colder winters of 1935–36 and 1950–51. The winter of 1950–51 killed all of more than a thousand larvae and pupae exposed except four, these becoming adult early in the winter.

In warehouses, however, temperatures within large bulks or stacks of bagged produce are not likely to fall as low as those recorded in the outbuildings, therefore a very cold winter would be necessary to kill any larvae occurring deeply in large masses of food which have entered storage during summer. Oxley (1948) has calculated that diurnal temperature changes will not penetrate more than six inches into a large bulk of grain. Unpublished observations by G. A. Brett confirm that protection is afforded by stacks of bagged products. During the rather warm winter of 1949–50, at a position only two bags from outside the stack, he obtained no temperatures below 7°C. at one warehouse and none below 4°C. at another, whereas in the same period the temperature fell to zero in the buildings used for the present experiments. He found that temperatures between 7° and 10°C. were prevalent for at least two months in the warmer stack, but judging from this paper these are unlikely to kill all the larvae present.

Infestation of the centre of a bulk or stack of produce will probably only occur when infested material is placed there initially at loading. Adults emerging inside stacks in the early winter are of no inportance in the warehouse, because adults can live for a mean of only 18 days at 10°C. and lay very few eggs at this or lower temperatures. Any eggs produced would die if exposed continuously to 10°C., and young larvae are killed by exposure for 13 days at 5°C., 5 days causing heavy mortality (fig. 3). Normal diurnal temperature fluctuation in warehouses at the surface of the food and in small buildings could sometimes afford conditions warm enough for free adult moths to lay eggs. However, during the comparatively warm winter period from October 1949 to February 1950 in the warmest unheated building used in this work, the temperature exceeded 10·5°C. for only 169 out of 3,480 hours. If eggs had been laid in this building and if any larvae had hatched from them, they would have died during three periods in which the temperature was continuously below 10·5°C. These lasted 17, 30 and 25 days, respectively, the second involving one period of six days with no temperature above 5·5°C.

The "mixed" culture, which was exposed in 1949–50 to the comparatively mild winter and to the spring in Building 3 (Table VI), produced spring adults giving rise to a dense culture by the autumn of 1950. Some larvae from the main experiments in Buildings 1 and 3 became adult after exposure to the mild winter of 1949–50 and incubation at 25°C. after the end of March. Only larvae surviving until the spring are important in small buildings as the adults produced would lay eggs at a time when the warm weather is beginning, resulting in a summer generation. In warehouses, some larvae became adult in Brett's unpublished experiments during 1949–50 on incubation after the end of March. Although the warmth of spring is slow to penetrate produce in large warehouses, temperatures probably become high enough to allow one or possibly two generations a year.

These considerations show that the normal British winter is not likely to eliminate infestations of *E. cautella* completely in large bulks or stacks of produce in warehouses. Heavy winter mortality can be expected depending in extent on the severity of the winter. The death rate can be increased by having windows open and leaving a space for air to circulate between rows of sacks in a stack. Larvae surviving the winter can give rise to a summer population.

The Infestation Control Division of the Ministry of Agriculture, Fisheries and Food have information of at least one instance of cross-infestation in winter.

In experiments, both at constant and variable temperatures, there has been considerable variation in resistance to cold between different batches of insects. Experiments have not been sufficiently detailed, however, to elucidate the main cause of this variation.

Batches of insects from different cultures of the same stock and also insects of different stocks have reacted differently to the same exposures to cold conditions. This indicates that factors operating during culturing have caused differences in the insects and also that there may be inherent differences in the stocks. It has been shown above that, in experiments at both constant and variable temperatures, no one stock was consistently more or less resistant than the others. This suggests that factors inherent in the stocks are not the main cause of variation.

Breeding at a constant favourable temperature for a long time can materially affect the insects, possibly by inbreeding or by the absence of natural selection. The insectary stock of *E. cautella* at this laboratory has become changed and proved most unsatisfactory for experiment due to a very high mortality even at favourable temperatures. Culturing the new stocks took place for two years, but the resistance to cold of these stocks showed no consistent relationship to the number of generations previously passed in culture.

The density of larvae in the breeding cultures varied considerably but this had no constant effect on resistance. For instance, larvae of stock III (Table VII) were bred in a culture containing only 27 mature larvae and a few smaller ones, but their resistance to the winter of 1950–51 was similar to the resistance of larvae from Culture A, stock IV (Table VII), which was a very crowded culture.

Death due to some form of shock may be caused by the rapid change of temperature involved when insects are moved from warm breeding conditions to cold outdoor and experimental conditions and back again. In most experiments, a period at an intermediate temperature was used to lessen the rate of change of temperature in order to decrease any shock effects.

Acclimatisation to temperatures near the lower end of an insect's temperature range may increase resistance to cold. Colhoun (1954) found that the cockroach, *Blattella germanica* (L.) survived longer at 7°C. after acclimatisation to 15°C. than to 25°C., which in turn produced a longer survival than acclimatisation to 35°C. Mellanby (1939) found that even short acclimatisation periods of 20 hours at warmer or cooler conditions within the normal range changed the temperature at which an insect is immobilised by cold, in some species by as much as 7·5°C. He also found that the temperature below freezing point which killed *Blatta orientalis* L. in a given short time was lower for insects acclimatised to 15°C. than for those acclimatised to 30°C. Acclimatisation was almost completed after only 20 hours. He had some evidence that acclimatisation to 15°C. also increased the resistance of this cockroach to longer exposures at temperatures above freezing point. In the present experiments the period at an intermediate temperature may have allowed some acclimatisation. However, any effect should be small because the breeding temperatures of 20° and 25°C. were within the lower half of the temperature range for complete development of *E. cautella.* Larvae from a culture of stock I (Table VII), which were bred in uncontrolled conditions during the summer and autumn of 1950 so that they were acclimatised to the moderately low temperatures of autumn, showed no greater resistance to the following winter than larvae of other stocks bred at a constant temperature.

Cold storage would be a practical method of control only for very valuable produce. Storage at 0°C. for one week would eradicate an infestation, providing that the low temperature penetrated the produce rapidly. Storage at 10°C. would prevent any increase in the number of insects present and would greatly reduce the activity of larvae. At 15°C. an infestation would increase extremely slowly.

Summary.

The effect of temperature on the life-cycle of *Ephestia cautella* (Wlk.) has been investigated, with emphasis on the effects of constant low temperatures and of the variable conditions of the English winter. The humidity was never low enough to have any effect on survival.

The total life-cycle (egg laid to adult) takes about 64 days at 20°C. and about 41–45 days at 25°C. on a wheatfeed-glycerine mixture.

The lowest temperatures at which the major changes in the life-cycle can be completed are:— hatching, 10° to 13°C.; pupation, 8·5°C.; and the change to adult, 10° to 13°C.

Large larvae are more resistant to cold than smaller larvae or eggs. The shortest exposures necessary to prevent large larvae from becoming adult are about one day at −1°C., five days at 0°C., 32 days at 5°C., or 83 days at 10°C.

Pupae can become adult at slightly lower temperatures than large larvae and also they can survive slightly longer exposures at −1°C.

Adult moths live for a mean of 18 days at about 10°C. Below this temperature adult life is shortened by cold, until at −1°C. moths survive for only one or two days. Adult life is also shortened at temperatures above 10°C., presumably by increased metabolism. At 35°C. adults live about three days. Copulation is infrequent at 13°C. and below, and few fertile eggs are laid at these temperatures. The highest number of eggs are laid at temperatures between 20°C. and 33°C.

Insects were exposed in a screen and in unheated outbuildings to the winters of 1949–50 and 1950–51. The overwintering stage is the large larva. Winter mortality was high. A few larvae became adult early in the winter; such survivals are of little importance as no progeny are likely to survive until the following summer. In outbuildings a few large larvae survived the winter of 1949–50. This is important since such larvae give rise to spring adults which lay eggs at the beginning of the warm weather. No larvae became adult after exposure in a screen to the winter of 1949–50, nor in either the screen or outbuildings after exposure to the winter and spring of 1950–51. Mansbridge (1936) obtained survival after exposure to the winter of 1934–35, but not after exposure to that of 1935–36. The winter of 1934–35 was warm, 1949–50 slightly colder, 1935–36 slightly colder than average and 1950–51 was cold. Several methods of comparing the severity of winter conditions in different buildings are described and discussed.

No single continuous period at temperatures below 10·5°C. occurred which was long enough to kill by itself all the larvae in the outbuildings. A method of summing the lethal effects of the hours experienced at low temperatures showed that a greater number of hours was necessary to kill larvae with these intermittent exposures, than with continuous exposure at any one low temperature.

In outbuildings possibly two generations per year can occur and a severe winter can eliminate a population.

Conditions in large warehouses are more protected and diurnal temperature changes scarcely penetrate large stacks of produce. In these conditions a normal winter would not eliminate a population deep in a large mass of food and there is a danger of cross-infestation to clean produce even in winter. Opening windows and leaving a space between rows of sacks in a stack are practical means of increasing winter mortality. Cold storage is an economic method of control only for very valuable produce.

Differences in resistance to cold between different batches of insects were encountered, but experiments were not sufficiently detailed to reveal the main causes of this variation.

Acknowledgements.

Thanks are due to Mr. G. A. Brett of the Infestation Control Division of the Ministry of Agriculture, Fisheries and Food for allowing me to quote his unpublished work and for providing stocks of moths, I, II and III, also to Miss M. B. Hyde of this Laboratory for allowing me to use her weather records for the screen.

This work forms part of the research programme of the Pest Infestation Laboratory, Slough, and is published by permission of the Department of Scientific and Industrial Research.

References.

BILHAM, E. G. (1938). The climate of the British Isles.—347 pp. London, Macmillan.

COLHOUN, E. H. (1954). Temperature acclimatization in insects.—Nature, Lond., **173,** p. 582.

FREEMAN, J. A. (1948). Stored-products pests: a survey of the principal entomological problems in the United Kingdom.—Ann. appl. Biol., **35,** pp. 294–301.

FUKAYA, M. (1939). Breeding experiments on *Ephestia cautella* Walk., with soybean refuse and rice bran. [*In Japanese.*]—Oyo-Dobuts. Zasshi, **11,** pp. 96–98. (Rev. appl. Ent., (A) **27,** p. 619.)

MANSBRIDGE, G. H. (1936). A note on the resistance to prolonged cold of some insect pests of stored products.—Proc. R. ent. Soc. Lond., (A) **11,** pp. 83–86.

MELLANBY, K. (1939). Low temperature and insect activity.—Proc. roy. Soc., (B) **127,** pp. 473–487.

METEOROLOGICAL OFFICE. (1934–52). Monthly Weather Report.—London, H.M.S.O.

NORRIS, M. J. (1934). Contributions towards the study of insect fertility. III. Adult nutrition, fecundity and longevity in the genus *Ephestia* (Lepidoptera, Phycitidae).—Proc. zool. Soc. Lond., **1934,** pp. 333–360.

OXLEY, T. A. (1948). The scientific principles of grain storage.—103 pp. Liverpool, Northern Publ. Co.

WASHBURN, E. W. *Ed.* (1928). International critical tables. Vol. 3.—New York & London, McGraw-Hill.

YATOMI, K. & YAMASHITA, S. (1938). On the effect of temperature and humidity upon the hatching of the eggs of *Ephestia cautella* Walk. (Preliminary report.) [*In Japanese.*]—Oyo-Dobuts. Zasshi, **10,** pp. 133–136. (R.A.E., (A) **26,** p. 671.)

TOXICITY AND INTERACTION OF STEREO-ISOMERS OF BENZENE HEXACHLORIDE IN COCKROACHES.

By K. van Asperen

Laboratory for Research on Biocides,
National Council for Agricultural Research, Utrecht.

In a former paper (van Asperen, 1954*a*) experiments on the interaction of the isomers of benzene hexachloride in albino mice were described and discussed. It was shown convincingly that the toxic effects of γ BHC are strongly antagonised by simultaneous administration of the δ or α isomer. The results were in full agreement with those of McNamara and Krop (1948*a*, *b*) but, for the present, one is not inclined to agree with their interpretation.

As BHC derives its practical importance from its strong insecticidal action, it was decided to investigate the same phenomenon by injection experiments with *Periplaneta americana* (L.), the American Cockroach. Before dealing with the results of these experiments some general principles of interaction have to be discussed.

Principles of Interaction.

Plackett and Hewlett (1952) suggested a set of models for the joint action of poisons, which they declared to be by no means exhaustive. Nevertheless, these models offer a valuable guide for the present discussion. These authors distinguished two main types of joint action, namely, similar joint action and dissimilar joint action. These two types can each be sub-divided according to whether interaction occurs or not.

Similar joint action is said to occur if two poisons elicit a certain quantal response by causing the same physiological system to react or fail. Dissimilar joint action is said to occur if two poisons elicit a certain quantal response by causing respectively different and distinct physiological systems to react or fail. Interaction of two poisons A and B is said to occur if the presence of A influences either the amount of B reaching B's site of action, or the changes produced by B at B's site of action.

If no interaction occurs and the toxicity of varying doses of two poisons is known, one may predict the toxicity of mixtures of the two in terms of mortality. For that purpose an assumption has to be made as to the type of joint action. In the case of *simple similar action*, which means similar joint action, as defined above, without interaction of the poisons, any given amount of one poison is equivalent to a certain amount of the other. If a dose r of the first poison is required to effect the same kill as a dose q of the second one, the joint action of a dose p of the first and a dose q of the second poison will result in a mortality equalling that resulting from a dose $p + r$ of the first poison. This mortality may be derived from the log dose–probit mortality regression line for the first poison.

Dissimilar joint action without interaction has been designated by the term *independent action*. Plackett and Hewlett (1952) pointed out that although the actions of the two poisons in this case are physiologically independent, the tolerances may be correlated. In other words, there may be no statistical independence. The correlation coefficient (ρ) may vary between the values -1 and $+1$. If a dose of the first poison, such as would result in a per cent. kill if

TABLE I.

Joint toxicity of γ and δ BHC.

No. of experiment	Dose (microgm./animal)		No. of animals		% mortality															
					After 1 day					After 3 days					After 6 days					
					Observed	Calculated				Observed	Calculated				Observed	Calculated				
	γ isomer	δ isomer	♂	♀	m_1	a_1	b_1	c_1	d_1	m_3	a_3	b_3	c_3	d_3	m_6	a_6	b_6	c_6	d_6
I	10 10 —	— 19 19	37 36 32	3 4 8	48 20 3	40	50	48	51	65 43 43	74	80	65	100	85 55 48	83	92	85	100
II	10 10 —	— 20 20	37 29 31	3 11 9	38 18 5	41	41	38	43	63 53 43	74	79	63	100	73 80 45	83	85	73	100
III	10 10 —	— 20 20	34 36 31	6 4 9	33 40 0	39	33	33	33	63 73 53	78	83	63	100	65 83 58	86	85	65	100
IV	10 10 —	— 20 20	31 29 33	9 11 7	23 30 8	42	29	23	31	68 70 53	78	85	68	100	70 75 53	84	86	70	100
V	5 5 —	— 10 10	40 40 40	— — —	30 25 8	30	36	30	38	45 45 35	60	64	45	80	55 60 38	69	72	55	93
VI	5 5 —	— 11 10	40 40 40	— — —	33 33 15	33	43	33	48	43 45 35	60	63	43	78	50 58 38	69	69	50	88
VII	5 5 —	— 5 5	40 40 40	— — —	20 20 0	24	20	20	20	35 33 8	48	40	35	43	40 40 8	57	45	40	48
VIII	5 5 —	— 5 5	40 40 40	— — —	28 33 3	26	30	28	31	43 40 13	50	50	43	56	53 50 13	59	59	53	66
IX	5 5 —	— 5 5	40 40 40	— — —	18 15 5	27	22	18	23	50 40 20	53	60	50	70	58 58 28	65	70	58	86

given alone, is combined with a dose of the second poison, such as would result in b per cent. kill if given alone, the mortality m resulting from administering a mixture of these doses may be calculated for different values of ρ.

$$\text{Assuming } \rho = +1 \text{ and } a > b$$
$$\text{then } m = a \tag{1}$$
$$\text{Assuming } \rho = 0$$
$$\text{then } m = a + b\left(\frac{100 - a}{100}\right) \tag{2}$$
$$\text{Assuming } \rho = -1 \text{ and } a + b < 100$$
$$\text{then } m = a + b \tag{3}$$

In each of these cases synergism will result in an increase of the mortality, whereas antagonism will decrease the mortality. If, however, a mortality between a and $a + b$ per cent. is found, this may be explained in a number of ways, each of which is more or less probable on physiological grounds. For example, assuming independent action with $\rho = +1$, the mortality would have been a per cent. Hence, to achieve a mortality greater than a, there must have been an increase of mortality from synergistic effects. If one assumes independent action with $\rho = -1$, the expected mortality would be $a + b$ per cent.; in this case, therefore, if a mortality $m < (a + b)$ results, antagonistic effects must have occurred. A third possibility is the absence of interaction, if the mortality actually found is what would be predicted for independent action and a particular value of the correlation coefficient. Further possibilities may be based on several models of similar joint action or intermediate types of joint action, some of which would have to include synergistic and others antagonistic effects.

As, however, the type of joint action can only rarely be inferred from physiological facts, it is mostly impossible to prove the occurrence of interaction. Only when the antagonistic or synergistic effects are very strong, will they be conclusively demonstrated by the mortality data obtained.

Thus, if the mortality actually found is less than a per cent., this can only be explained by assuming antagonistic effects. Any model lacking antagonism would result in higher mortalities, somewhere between a and $a + b$, if there is no interaction at all, or exceeding $a + b$ per cent., if synergistic effects come into play.

Experimental.

Adult cockroaches were injected by inserting the injection needle between the sternites of the 5th and 6th abdominal segments and then delivering 40 microl. of an emulsion prepared by dissolving a known amount of BHC in peanut oil and emulsifying 1 ml. of this solution with 49 ml. of physiological salt solution with the aid of an emulsifier. As there is a rather large difference in susceptibility between males and females, in most experiments only males were used.

In order to avoid sampling errors as much as possible, the test animals available for an experiment were divided arbitrarily into two or three groups. The animals of the first group received a certain amount of the γ isomer, those of the second group the same amount of the γ isomer and in addition a certain amount of δ or α BHC. A third group received the same quantity of the δ or α isomer alone.

Results.

Table I gives the data obtained in the experiments using δ and γ BHC. Table II gives the data for the experiments using α and γ BHC. The mortalities were determined one, three and six days after injection. The values calculated

TABLE II.

Joint toxicity of γ and α BHC.

No. of experiment	Dose (microgm./animal)		No. of animals		% mortality														
					After 1 day					After 3 days					After 6 days				
					Observed	Calculated				Observed	Calculated				Observed	Calculated			
	γ isomer	α isomer	♂	♀	m_1	a_1	b_1	c_1	d_1	m_3	a_3	b_3	c_3	d_3	m_6	a_6	b_6	c_6	d_6
I	5	—	40	—	33	36	46	33	53	45	60	64	45	80	53	69	71	53	91
	5	8	40	—	40					50					60				
	—	8	40	—	20					35					38				
II	5	—	40	—	23	30	29	23	31	35	56	51	35	60	40	67	60	40	73
	5	8	40	—	23					35					53				
	—	7	40	—	8					25					33				
III	5	—	40	—	30	27	34	30	35	50	53	59	50	68	55	62	64	55	75
	5	5	40	—	30					43					60				
	—	5	40	—	5					18					20				
IV	5	—	35	—	17	24	17	17	17	37	48	41	37	43	43	59	51	43	57
	5	5	40	—	13					30					40				
	—	5	35	—	0					6					14				

according to several models of joint action are also given for comparison. Only models without interaction have been dealt with.

The mortalities for independent action with values of ρ equal to $+1$, 0 and -1 were calculated from equations (1), (2) and (3) above.

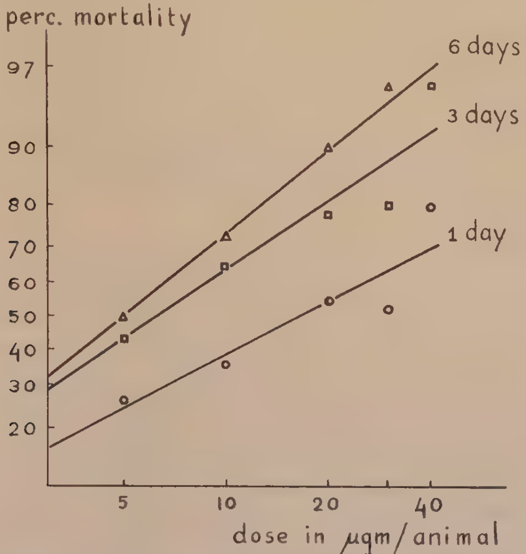


Fig. 1.—Mortality in *Periplaneta americana*, one, three and six days after the injection of γ benzene hexachloride. Abscissae: log dose of the poison. Ordinates: probit mortality.

The calculations of the mortality in the case of simple similar action were based on the regression lines for the γ isomer (fig. 1). The following example illustrates the method used. In experiment IV (Table I) the injection of 20 microgm. of δ BHC resulted in a mortality of 53 per cent. after three days. This mortality would have been caused by a dose of 7 microgm. of γ BHC. The injection of a mixture of 10 microgm. of γ BHC and 20 microgm. of δ BHC would thus be expected to correspond with the injection of 17 microgm. of the γ isomer, and from the regression line this would result in a mortality of 78 per cent.

Discussion.

The mortality values (m) actually found after simultaneous injection have been compared with those obtained by calculation for four theoretical possibilities, namely: simple similar action, (a); independent action with $\rho = 0$, (b); independent action with $\rho = +1$, (c); and independent action with $\rho = -1$, (d). The following conclusions can be drawn:—

1. The mortalities actually found after three and six days (m_3 and m_6, respectively) are in every case in Tables I and II lower than those calculated for simple similar action (a_3 and a_6, respectively), for independent action with $\rho = 0$ (b_3 and b_6, respectively) and for independent action with $\rho = -1$ (d_3 and d_6, respectively). When these differences ($m_3 \sim a_3$, $m_3 \sim b_3$, etc.) over the nine experiments included in Table I are subjected to the sign test * (Dixon & Massey,

---

* A test depending on the probability that, in a series of separate comparisons of two quantities, one will exceed the other by chance in a given number of cases.

1951), they are found to be significant at $P<0{\cdot}01$. There are insufficient experiments in Table II for this test to be applied.

2. There is good overall agreement between the data actually obtained and those calculated for independent action with $\rho = +1$, (c_3 and c_6). This is particularly the case in the last five experiments of Table I and all those of Table II, in which only males were used. In the first four experiments of Table I, the interpretation of the results is complicated by the fact that different numbers of females were present in the groups of test animals, but in spite of these few deviating observations, independent action with a complete or nearly complete positive correlation of the tolerances for the two poisons is, of those so far considered, the only type of joint action giving an appropriate explanation of the mortality data obtained. When the differences $m_3 \sim c_3$ and $m_6 \sim c_6$ in Table I are subjected to the sign test, they are not significant, the value of P being $>0{\cdot}25$ in both cases.

Statistically speaking, this explanation may be considered quite satisfactory. From a physiological point of view, however, it is not very probable that the susceptibilities to two poisons which act independently and thus have quite different sites of action in the body, would parallel each other completely. Although this explanation should not be rejected, other explanations may be looked for. Having regard to the relatively low mortalities after combined doses and the strong antagonism found in mice (van Asperen, 1954), one is inclined to assume the occurrence of antagonistic effects. Two types of antagonism may be suggested to have played a part in the experiments.

1. Antagonism of the γ isomer by the α or δ isomer. Evidently, if this action has occurred, its effect has been to reduce the toxicity of the γ isomer, but not to nullify it.
2. Antagonism of the α or δ isomer by the γ isomer. As the mortality from combined doses equals that from the γ isomer alone, the effect of the antagonism, if it has occurred, has been completely to nullify the α and δ isomers.

Whereas the results obtained after simultaneous injection of the isomers in mice can be explained only by the first type of interaction, in *P. americana* both the first and the second type can give an appropriate explanation of the data. Moreover it is possible and, in these experiments, even rather probable, that there exists a mutual antagonism between the α or δ isomer and the γ isomer.

Undoubtedly the possible antagonistic effects in *P. americana* are much weaker than those occurring after simultaneous injection of BHC isomers in mice, or, at least, they are less clear. This may be caused by the fact that α and δ BHC are considerably more toxic in cockroaches than in mice.

As to the nature of these antagonistic effects, no positive conclusions can be drawn. The chemical structures of the isomers being at least partly similar, one is inclined to propose some kind of competitive inhibition. The physiological background of the interaction-effects have been discussed in previous papers (van Asperen, 1954 *a*, *b*).

Summary.

Some types of joint action of insecticides described by previous authors are discussed, and experiments described on the joint action on *Periplaneta americana* (L.) of the γ and δ isomers, and of the γ and α isomers, of benzene hexachloride. The values of the mortalities obtained are given in tables and compared with calculations of those that would be expected according to several models of joint action in which no interaction occurs. From statistical evidence it is concluded that only one of these models, namely, independent action with a strong positive correlation of the susceptibilities to the two poisons, can give an

appropriate explanation of the results. These results, however, can also be explained by suggesting that antagonistic effects play a part in the joint action of the BHC isomers investigated.

Acknowledgements.

Dr. C. Potter and Mr. M. J. R. Healy of Rothamsted Experimental Station have been so kind as to read through the manuscript. Their valuable remarks have been highly appreciated.

The author wishes to thank Dr. D. Dresden for his advice and criticism and to acknowledge the help in the statistical treatment received from Dr. E. F. Drion of the Statistics Department T.N.O. My thanks are also due to the late Miss C. van Donkelaar for her valuable technical assistance.

References.

van Asperen, K. (1954*a*). Arch. int. Pharmacodyn., **99**, pp. 368–377.

van Asperen, K. (1954*b*). Meded. LandbHogesch. Gent, **19**, pp. 536–545.

Dixon, W. J. & Massey, F. J. (1951). Introduction to statistical analysis.—New York, McGraw-Hill.

McNamara, B. P. & Krop, S. (1948*a*). J. Pharmacol., **92**, pp. 140–146.

McNamara, B. P. & Krop, S. (1948*b*). J. Pharmacol., **92**, pp. 147–152.

Plackett, R. L. & Hewlett, P. S. (1952). J. R. statist. Soc., (B) **14**, pp. 141–163.

THE NOMENCLATURE AND LIFE-CYCLE OF THE EUROPEAN TARNISHED PLANT BUG, *LYGUS RUGULIPENNIS* POPPIUS (HEM., MIRIDAE).

By T. R. E. Southwood

12 *Department of Entomology, Rothamsted Experimental* E.F.
Station, Harpenden, Herts.

Nomenclature.

Subsequent to Uhler's (1886) check list and prior to 1941, the vernacular name "Tarnished Plant Bug" was applied throughout the Holarctic region to Mirid (or Capsid) bugs which were considered to represent one species, namely *Lygus pratensis* (L.). In 1941, Knight raised the Nearctic form *oblineatus* (Say) 30 to specific rank; American workers have generally adopted this as the scientific name of the Tarnished Plant Bug and this course was followed in the most recent distribution map (Commonw. Inst. Ent., 1954*a*). Slater & Davis (1952) have 42 shown, however, that *L. oblineatus* (Say, 1832) is synonymous with *L. lineolaris* (P. de B., 1818) and should in fact be known by that name.

Meanwhile in Europe, Kullenberg (1941), Wagner (1941) and Leston (1951) have raised *L. pratensis* var. *pubescens* Reut., 1912 to specific rank. Linnavouri (1951), followed by China (1951), has shown, however, that this species is synonymous with *L. rugulipennis* Popp., 1911, although Kirichenko (1951) erroneously keeps them as separate species.

In most cases, therefore, one cannot be certain whether biological and economic records of *L. pratensis* in the Palaearctic really refer to this species or to *L. rugulipennis*. Only the better known name, *pratensis*, was used in the latest list of common names of British insects (Ass. Appl. Biol., 1952) and a recent distribution map (Commonw. Inst. Ent., 1954*b*); but such evidence as there is indicates conclusively that although both may occur on crops, *L. rugulipennis* is a much more important pest.

Surveys of crop pests in which *L. rugulipennis* is distinguished from *L. pratensis* are unfortunately few. Ossiannilsson (1943) recorded both species from potatoes in Sweden, but *L. rugulipennis* was more abundant and widespread; whilst Balcells (1949) found only the latter species on potatoes in Spain. Blattný, Kac & Hoffer (1948) mention both species as pests of lucerne in Czechoslovakia, but Nuorteva & Veijola (1954) found *L. rugulipennis* easily the more important as a pest of wheat in Finland. Drs. Cobben (Holland), Ossiannilsson (Sweden) and Remane (Germany) have kindly informed me (*in litt.*) that *L. rugulipennis* is certainly the more abundant species on crops in their countries. Through the kindness of Mr. V. Fowler, I have examined 22 specimens of the Tarnished Plant Bug collected by the late Mr. G. Fox Wilson, mostly from chrysanthemums, which all proved to be *L. rugulipennis*; whilst a general collection made by M. V. L. Pjatokova at Mleev, Kiev Province, S. Russia and now in the British Museum (Nat. Hist.) was found to consist of 40 *L. rugulipennis* and only three *L. pratensis*. In four (1946–49) years' light-trapping at Rothamsted Experimental Station, Harpenden, only four *L. pratensis* were captured compared with 1,771 *L. rugulipennis*; field collecting also confirms the much greater abundance of the latter.

It can be concluded, therefore, that *L. rugulipennis* is the more important pest in the Palaearctic region and that it is to this species that the name

European Tarnished Plant Bug should properly be applied. It has also been recorded from Alaska (Leston, 1952).

Wagner (1949, 1950, 1952) considers that besides *L. rugulipennis* there are four other European species confused under the name *L. pratensis*, namely *L. pratensis*, *sens. str.*, *L. gemellatus* (H.-S.), *L. maritimus* Wagn. and *L. rutilans* Horv. Both Kullenberg (1946) and Leston (1952) have suggested that these are ecological or climatic forms, but Slater & Davis (1952) have found evidence from the female genitalia which strengthens the view that Wagner is correct. Work is, however, being carried out elsewhere on this problem and on the classification of the genus *Lygus* Hahn. All the species discussed above are included in the same subgenus, at present known as *Exolygus* Wagn., which contains part of *Apolygus* China (Leston, 1952).

Life-cycle.

In view of the above it is uncertain to what extent previous work on *L. pratensis* can be referred to *L. rugulipennis*. Austin (1931, 1932) and Wilson (1938) showed that *L. pratensis* generally overwintered as an adult and had more than one generation a year, but Ossiannilsson (1943) doubted whether adults of *L. pratensis* or *L. rugulipennis* could survive the winter in Sweden.

Samples of litter taken at Rothamsted between autumn 1952 and the following spring often contained specimens of *L. rugulipennis*. During late April and May 1953 both males and females of this species were collected by sweeping and some of these (2 ♂♂, 5 ♀♀) were kept in the open in muslin cages on potted plants of *Plantago major*. On 11th June larvae of the first and second instar were present with four overwintered females, the latter were marked with cellulose paint and were still alive on 7th July together with fourth- and fifth-instar larvae and many adult males and females of the summer generation. Two of the overwintered females were dissected; their ovaries had atrophied showing that they could no longer be considered as belonging to the reproductive population. One of the remaining overwintered females was still alive on 10th August, by which date the larvae of the autumn generation (its " grandchildren ") were in the first and second instar. These larvae matured in September and the last adults of the summer generation died early in October.

From these observations it can be seen that the life-cycle of *L. rugulipennis* in England agrees with that previously described by Austin (1931, 1932), Wilson (1938) and others for *L. pratensis*. Some of the apparent confusion over the number of generations could well be due to the long post-reproductive life of the females found in this work.

Thus the following is a summary of the life-history of the European Tarnished Plant Bug, *Lygus rugulipennis*, in England. There are normally two generations a year: the summer one maturing at the end of July from eggs laid in the spring (about May), and the autumn one in September. This generation engages in considerable flight activity (Johnson & Southwood, 1949) before overwintering amongst leaves and débris in hedge bottoms and similar situations. In the autumn, the population of the species is at its highest level, but is considerably reduced during hibernation.

Summary.

Recent taxonomic studies have recognised that *Lygus pratensis* (L.) consists of several species and other workers have shown that the Tarnished Plant Bug of N. America is *L. lineolaris* (P. de B.), a species confined to that continent. Although it is impossible to be certain what species is referred to in all of the earlier works on biology and pest incidence of *L. pratensis* in the Palaearctic region, evidence is given which shows that *L. rugulipennis* Popp. is the more

important pest in this region and it is to this species that the name European Tarnished Plant Bug should be applied. Observations on the life-cycle of *L. rugulipennis* in England have been carried out and they show that there are normally two generations per year; the second generation becomes adult in the autumn and overwinters in this stage, egg-laying occurring the following spring. This agrees in general with that previously described for *L. pratensis*, *sens. lat.*

References.

Ass. Appl. Biol. (1952). Common names of British insect and other pests. Part two.—40 pp. [Harpenden, Herts.]

Austin, M. D. (1931). Observations on the hibernation and spring oviposition of *Lygus pratensis* Linn.—Ent. mon. Mag., **67**, pp. 149–152.

Austin, M. D. (1932). A preliminary note on the Tarnished Plant Bug (*Lygus pratensis* Linn.).—J. R. hort. Soc., **57**, pp. 312–320.

Balcells, R. E. (1949). Algunos insectos vectores de virus en cultivos de patata. (Nota previa.)—Rev. Ilerda, **12–13**, pp. 105–151.

Blattný, C., Kac, A. & Hoffer, A. (1948). Pozorování a pokusy s pěstováním vojtěšky na semeno, zejména s ohledem na boj proti plodomorce vojteškové a j. škodlivým činitelům vojtěšky.—Ochr. Rost., **19–20**, pp. 40–46.

China, W. E. (1951). Note on *Lygus* (*Exolygus*) *pubescens* Reuter (Hem., Miridae).—Ent. mon. Mag., **87**, p. 319.

Commonw. Inst. Ent. (1954*a*). *Lygus oblineatus* (Say).—Distr. Maps Ins. Pests, (A) no. 38.

Commonw. Inst. Ent. (1954*b*). *Lygus pratensis* (L.).—Distr. Maps Ins. Pests, (A) no. 39.

Johnson, C. G. & Southwood, T. R. E. (1949). Seasonal records in 1947 and 1948 of flying Hemiptera-Heteroptera, particularly *Lygus pratensis* L., caught in nets 50 ft. to 3,000 ft. above the ground.—Proc. R. ent. Soc. Lond., (A) **24**, pp. 128–130.

Kirichenko, A. N. (1951). True Hemiptera of European U.S.S.R. Key and bibliography. [*In Russian.*]—Opred. Faune SSSR, no. 42, 423 pp. Moscow, Akad. Nauk SSSR.

Knight, H. H. (1941). The plant bugs, or Miridae, of Illinois.—Bull. Ill. nat. Hist. Surv., **22**, pp. 1–234.

Kullenberg, B. (1941). Ueber die Aufteilung von *Lygus pratensis* (L.).—Ent. Tidskr., **62**, pp. 177–183.

Kullenberg, B. (1946). Studien über die Biologie der Capsiden.—Zool. Bidr., **23**, p. 1–522.

Leston, D. (1951). *Lygus pubescens* Reuter, a Mirid (Hem.) new to the British list.—Ent. mon. Mag., **87**, pp. 244–246.

Leston, D. (1952). On certain subgenera of *Lygus* Hahn 1833 (Hem., Miridae), with a review of the British species.—Ent. Gaz., **3**, pp. 213–230.

Linnavuori, R. (1951). Hemipterological observations.—Ann. ent. fenn., **17**, pp. 51–65.

Nuorteva, P. & Veijola, T. (1954). Studies on the effect of injury by *Lygus rugulipennis* Popp. (Hem., Capsidae) on the baking quality of wheat.—Ann. ent. fenn., **20**, pp. 65–68.

Ossiannilsson, F. (1943). Studier över de svenska potatisfältens insektfauna och dess betydelse för spridning av virussjukdomar. I. Hemiptera, förehomst och utbredning.—Medd. Växtskyddsanst., no. 39, 72 pp.

Slater, J. A. & Davis, N. T. (1952). The scientific name of the Tarnished Plant Bug (Hemiptera, Miridae).—Proc. ent. Soc. Wash., **54,** pp. 194–198.

Uhler, P. R. (1886). Check-list of the Hemiptera Heteroptera of North America.—34 pp. Brooklyn.

Wagner, E. (1941). Zur Systematik von *Lygus pratensis* L.—Verh. Ver. naturw. Heimatforsch., **28,** pp. 149–154.

Wagner, E. (1949). Zur Systematik der Gattung *Lygus*.—Verh. Ver. naturw. Heimatforsch., **30,** pp. 26–40.

Wagner, E. (1950). Die Artberechtigung von *Lygus maritimus* E. Wagn. (Hem. Het. Miridae).—Ent. Ber., **13,** pp. 87–90.

Wagner, E. (1952). Blindwanzen oder Miriden.—Tierwelt Dtsch., **41,** 218 pp.

Wilson, G. Fox (1938). The Tarnished Plant Bug or Bishop Fly, *Lygus pratensis* L.—Précis of present knowledge.—J. R. hort. Soc., **63,** pp. 392–395.

THE PERSISTENCE AND FATE OF DDT ON FOLIAGE.

II.—COMPARATIVE RATES OF LOSS OF DDT DEPOSITS FROM GLASS PLATES AND GROWING LEAVES.

By J. WARD and P. E. BURT

Department of Insecticides and Fungicides,
Rothamsted Experimental Station, Harpenden, Herts.

E.H.N. 1.

Introduction.

In the first part of this work (Burt & Ward, 1955) it was shown that DDT was appreciably volatile at temperatures likely to be reached by foliage in full sunlight, that the rate of volatilisation was sufficient to cause, in one or two weeks, a serious reduction in the toxicity of a deposit of DDT crystals applied to glass plates at a rate of 10 microgm. per sq. cm. or less, and that when the deposit was lying on a thin layer of plant wax applied to the glass plates it did not become dissolved to an appreciable extent in the wax, except when the plates were stored in an atmosphere saturated with DDT vapour. Even though the amount of DDT in solution in the wax at any time is only a small proportion of the total, diffusion through the wax may still be an important cause of loss of activity of a deposit of DDT on a leaf surface if the DDT is continuously removed from the wax layer by further penetration into the plant tissues.

The ease with which most of a deposit of DDT on a leaf can be removed by washing with benzene was not considered to be sufficient proof that the DDT was mainly on the surface, as organic solvents themselves readily penetrate into the leaf, presumably through the stomata. We have not been able to devise a method of washing which will remove superficial DDT with certainty, but which can be shown not to remove DDT from inside the leaf. It was therefore decided

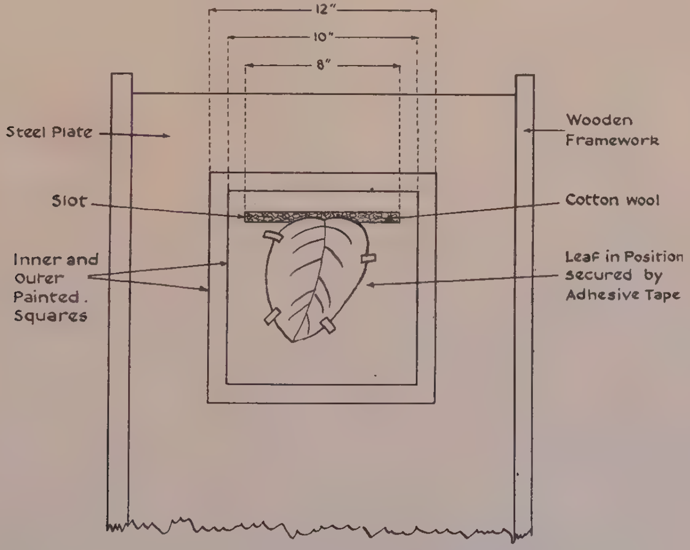

12"
10"
8"
Steel Plate
Wooden Framework
Slot
Cotton wool
Inner and Outer Painted. Squares
Leaf in Position Secured by Adhesive Tape

Fig. 1.—Steel plate with leaf in position for spraying. (See fig. 2.)

to study the rate of loss of DDT and of contact toxicity from deposits on leaves of various species of plants, to see whether loss of toxicity was greater on leaves than it was on similarly exposed glass plates.

Methods.

Application of insecticide to foliage.

As it was desired to study the loss of DDT from deposits on leaves for periods up to six weeks, a means of spraying leaves *in situ* on plants was necessary. The method was required to produce a very even deposit over the whole area sprayed, because only small fractions of each leaf area could be tested biologically, and the rates of the deposits applied had to be accurately known and reasonably predictable. A method fulfilling the above requirements was devised, in which the operator discharged insecticide from a spray-gun at a steel target plate supporting the foliage to be sprayed.

The steel plate (see fig. 1), 20 × 28 in., was set vertically on a bench in such a position that its upper part was level with the chest of the operator. On the plate was painted a square 12 × 12 in. and symmetrically inside this another square 10 × 10 in. Just below the upper edge of the inner square and extending nearly across its width, a slot was cut in the steel plate. A square frame (see fig. 2) was constructed, three sides of which were of wood, the fourth and uppermost side of wire. This was supported so that it stood parallel to the steel plate, 12 in. distant from it, and coaxial with the painted squares on the plate.

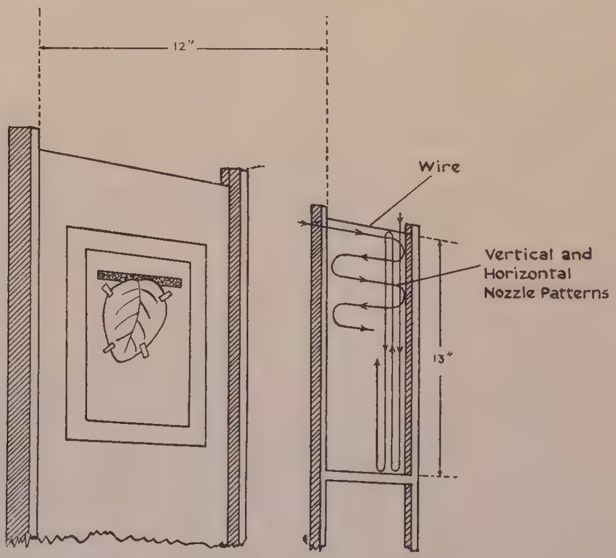


Fig. 2.—Apparatus for spraying leaves with insecticide while still attached to plants, showing relationship between the target plate and the frame through which the spray is discharged. Lines show the track followed by the spray nozzle.

The fourth side was of wire, in order to obscure the plate as little as possible when aiming the spray-gun. The spraying apparatus was an Aerograph M.P. spray-gun running at a pressure of 25 lb. per sq. in., with suitable liquid and air supply adjustments and an arrangement to hold the trigger in the " on " position when required, to avoid unintentional variations in trigger pressure. The procedure was as follows:—

The pot containing the plant to be sprayed was supported on its side on a stand behind the steel plate, and one or more of the plant's leaves were pushed through the slot in the plate and taped down lightly so that they lay as flat as possible against the plate's surface. All foliage to be sprayed was sited inside the inner painted square. To prevent chance contamination when spraying the foliage, the rest of the plant was covered with a clean cloth and the unoccupied part of the slot was blocked up with cotton-wool. The operator then charged the spray-gun reservoir and a known volume of liquid was discharged at the steel plate. During spraying, the gun was moved in such a way that the nozzle described a pattern inside the wooden frame (see fig. 2), the nozzle being kept in the plane of the wood and wire frame so as to ensure a constant distance between nozzle and target, with its axis as nearly as possible perpendicular to the target plate. Each complete DDT deposit was built up by applying at least four coats of sprayed material, and each coat was dried off with hot air from a hair-dryer before the next was applied. Alternate coats were applied with horizontal and vertical movements of the nozzle, thus distributing the deposit as evenly as possible. The cone of spray traversed the whole of the 12-in. square on the target plate, but only the deposit on the inner 10-in. square was used in the experiments; the edges were insufficiently uniform.

An estimate of the evenness of the deposit produced was obtained by spraying sets of nine glass plates, that together almost covered the inner 10-in. square, with dye solution or DDT suspension, and determining the deposit on each plate analytically. This procedure was repeated several times by each spray operator. The standard deviation was calculated for each set of nine glass plates and, for experienced operators, averaged 6 per cent. In another experiment, glass plates and leaves from cabbage, laurel, dock and *Cineraria* were sprayed with DDT suspension. Discs were cut from the leaves, of the size used subsequently for bioassay, and the deposit densities on these and on the glass plates were determined; it was found that the rates of deposit on the five different surfaces did not differ significantly. The standard deviation of the deposits on the leaf discs was 10 per cent. A somewhat larger figure than that found for the sampling area of the glass plates (67 sq. cm.) was to be expected for the leaf discs (area 5·5 sq. cm.). These standard deviations refer only to plates or leaf discs sprayed simultaneously; the variation in deposit density between spraying operations was fairly large, due to variations in the rate of discharge of the spray gun, to the effects of temperature and humidity on the proportion of the spray droplets impacting on the target, and to personal factors introduced by the operator. Hence, whenever foliage was sprayed, glass plates were attached to the target plate and analysed to give the actual rate of application.

Materials sprayed.

In all experiments except one the DDT formulation used was a suspension of DDT crystals, needle-shaped and approximately 50 μ long, in a 0·1 per cent. solution of Sulphonated Lorol in 10 per cent. ethanol and 90 per cent. water, prepared according to the method of McIntosh (1947). The concentrations of DDT varied from 0·1 per cent. downwards. When heavier deposits were required, equivalent to four coats of a 0·2 per cent. suspension of DDT, it was found that this concentration of DDT tended to block the spraying jet. The desired rate of deposit was therefore obtained by spraying eight coats of a 0·1 per cent. suspension of DDT containing only 0·05 per cent. Sulphonated Lorol, so that the final concentration of Sulphonated Lorol in the deposit was the same as that produced when other concentrations of DDT were sprayed. All solutions used in the preparation of suspensions were filtered to avoid blocking the spray-gun nozzle.

In one experiment, an emulsion was used. It was prepared by emulsifying a

25 per cent. w/v solution of DDT in xylene with a non-ionic wetting agent (Agral LN) and diluting with sufficient water to make the concentration of wetting agent 0·1 per cent. Recrystallised p,p′DDT, M.P. 106–107°C., was used for both types of formulation.

Plants used.

The plants used were selected with a view to testing as many types of foliage surface as possible; they were cabbage (very waxy surface), *Cineraria* and marrow (hirsute surfaces), strawberry (less waxy and slightly hirsute), dock (smooth and less waxy).

Assay of deposits.

The method used for the biological assay of DDT deposits on foliage was a modification of a technique suggested by M. J. Way (private communication). Leaf discs were cut from the sprayed leaves and adult *Tribolium castaneum* (Hbst.) were confined on their surfaces for 24 hours at 18°C. by means of small glass collars, 1 in. diameter and approximately 1 in. high. The leaf discs were kept turgid by supporting them on filter paper kept moist by small pieces of wet cotton-wool. The glass collars were held tightly in contact with the leaf discs by rubber bands stretched over their tops and secured to the mounting board by strong pins. Deposits on glass plates used for comparison with the leaves were tested in a similar fashion, the glass collars being secured to the plates by small drops of paraffin wax, applied to the outside of the circles so as to avoid contamination of the test area. Ten insects were placed inside each glass collar on the test surface, and normally four replicates were used for each deposit tested, whether on glass or leaf surfaces.

After remaining 24 hours on the test surfaces, the insects were removed, by means of a suction trap connected to a filter pump, to specimen tubes where they were kept a further three days at 18°C. before being examined on a warm plate and the dead counted.

The insects were reared at a temperature of 27°C. and whenever tests were carried out simultaneously, insects of the same age were used so that results might be directly comparable, but insects of the same age were not used throughout all the experiments.

The method of chemical estimation of the DDT deposits on leaves was as follows: the leaf samples were heated with benzene in a boiling-tube; when the benzene boiled, it was poured off, the pieces of leaf were washed twice with cold benzene, the benzene extracts were combined, and the DDT determined by the method used for glass plates (Burt & Ward, 1955). This method of extraction removed the wax from the leaf, and it was assumed that the extract would contain all the superficial DDT, together with any which might be dissolved in the wax layer. The proportion so dissolved was expected to be small, for when glass plates coated with cabbage wax were kept in contact with DDT crystals for periods up to 14 days, the proportion of DDT dissolved in the wax was never large (Burt & Ward, 1955).

The methods of presenting the results differed from one experiment to another and will be explained as each is described.

Inherent Toxicity of Surfaces.

Before studying the effects of exposure on DDT deposits on glass plates and on various kinds of foliage, it was necessary to determine the initial toxicity of given rates of deposit on each of these surfaces. Glass plates and several species of leaves were sprayed with a graded series of concentrations of DDT. Each surface was tested for toxicity to *T. castaneum*, and dosage-mortality curves were constructed from the data by the probit transformation (Bliss, 1934; Finney, 1947). The log LD50's of the various regression lines were then compared. The results from three of these leaf-comparison experiments are summarised in Table I.

TABLE I.

Toxicity of DDT deposits to adult *T. castaneum* on various leaf surfaces and on glass plates. LD50 in microgm. per sq. cm. with log (LD50 × 10) and standard error.

Nature of surface	Experiment 1		Experiment 2		Experiment 3	
	LD50	Log LD50	LD50	Log LD50	LD50	Log LD50
Marrow	—	—	—	—	0·45	0·65±0·02
Cabbage	—	—	0·46	0·66±0·05	0·50	0·70±0·10
Dock	0·66	0·82±0·09	—	—	0·62	0·79±0·02
Strawberry	—	—	0·54	0·73±0·03	—	—
Laurel	0·47	0·67±0·06	—	—	—	—
Cineraria	0·49	0·69±0·04	—	—	—	—
Plates	—	—	1·0	1·00±0·06	1·0	1·00±0·04

The results showed that differences in toxicity between the various leaf surfaces were very small, and were similar in magnitude to the experimental errors of the test methods, but that the deposits on leaves were all more toxic than those on glass. Thus the LD50 for deposits on leaves ranged from 0·45 to 0·66 microgm. per sq. cm., whereas the LD50 on glass, in each of the two experiments in which it was determined, was 1·0 microgm. per sq. cm. It is believed that this greater toxicity of films on leaves than on glass is connected with the greater humidity of the environment of the insects exposed to deposits on leaves.

Effect of Humidity of Test Surfaces.

There is evidence (Pradhan, 1949*a*, *b*) that the toxicity of DDT is influenced by the temperature and humidity of the surrounding air while the insects are in contact with the toxicant. Variations in toxicity due to temperature effects were avoided by doing the experiments in a constant-temperature room, but it was possible that differences in humidity, due to the transpiration of the leaf discs, could have occurred. Pradhan (1949*b*) concluded that there was a positive correlation between humidity and toxicity of DDT deposits to adults of *T. castaneum*; this would offer an explanation for the higher toxicities recorded on leaf surfaces.

In each of two experiments, adults of *T. castaneum* were exposed at two air humidities to glass or Cellophane surfaces bearing DDT deposits. The method of achieving the upper level of humidity in the first experiment was to insert plugs of damp cotton-wool into the tops of the glass collars confining the test insects on the glass plates; in the second experiment, discs of Cellophane were mounted for testing and kept damp in the same way as has been described for leaf tests. The lower level of humidity was provided by the atmosphere of the constant-temperature room (60% R.H.). A comparison kill was obtained at this humidity on glass surfaces only for the first experiment, and on both glass and dry Cellophane surfaces for the second. Each experiment was carried out using several concentrations of DDT, in such a way as to permit analysis of the results by the probit method. The results are summarised in Tables II and III. They are expressed as log relative potencies of the deposits, the potency on glass at room humidity being taken as unity. The log relative potency of a deposit on a particular surface for a given set of conditions is calculated by subtracting the corresponding log LD50 from the log LD50 of a deposit on glass under the standard conditions of the constant-temperature room.

TABLE II.

Log relative potency, with standard error, of DDT deposits on glass surfaces when the humidity of the air is maintained at a high level during exposure of *T. castaneum*. Potency of deposits at room humidity (60%) taken as unity.

Experiment no.	Relative potency	Log relative potency
1	1·95	+0·29±0·08
2	1·15	+0·14±0·04
3	1·70	+0·23±0·10

The results in Table II show an increase in toxicity under the conditions of increased humidity which is roughly similar to the average difference found between leaves and plates (see Table I). The results in Table III show that a deposit on dry Cellophane is more toxic than the same deposit on glass, and that when the Cellophane is kept moist, the deposit becomes even more toxic. The difference between the log potencies of deposits on moist Cellophane and on dry averages 0·31; this is very close to the difference between the log potencies of deposits on glass and on leaf surfaces, which averages 0·29 in experiments 2 and 3 (Table I). It seems likely, therefore, that the increased toxicity of a deposit on a leaf surface, as compared with glass, is due to the effect on the test insects, or on the deposit itself, of the increased humidity of such an environment. In the work described below, therefore, deposits on glass plates were used only for reference and comparison and not as indicators of the kill to be expected from deposits on leaves.

TABLE III.

Log relative potency, with standard error, of DDT deposits on damped Cellophane and on Cellophane at room humidity, using *T. castaneum*. Potency of deposits on glass at room humidity taken as unity.

Experiment no.	Cellophane, room humidity		Cellophane, damped	
	Relative potency	Log relative potency	Relative potency	Log relative potency
1	3·3	+0·52±0·28	5·3	+0·72±0·03
2	1·7	+0·22±0·08	4·4	+0·64±0·16

The difference between the toxicity shown by deposits on dry Cellophane and on glass is not fully understood; such unexpected differences have been encountered previously in the work, *e.g.*, that between deposits on sisal wax and on cabbage wax (Burt & Ward, 1955). In the present case, it may be that the Sulphonated Lorol in the spraying suspension is partly absorbed by the Cellophane, and that the crystals are consequently less adherent to their support and more readily detached by the test insects.

Change of Toxicity of Deposits on living Leaves with Time.

Loss of crystalline DDT at air temperatures of 10–21°C.

Three species of plant were used in this experiment: dock, cabbage and marrow. They were sprayed with suspensions of DDT at three different concentrations, and were kept for periods of 37, 24, and 6 days in a heated greenhouse where the temperature ranged from 10° to 21°C. The leaves had to be sprayed *in situ* on the plant and, since this is a slow and laborious process, the number of leaves which could be sprayed was limited. Glass plates were sprayed with each leaf, and one from each spraying was analysed to give the rate of deposit.

Leaf growth during the experiment was measured by marking each leaf with four spots of white ink, representing the corners of a rectangle of known size. Before the leaves were assayed the rectangles were measured and the increase in area noted. The DDT remaining on the various surfaces was assayed both biologically and chemically on the same day. A reference level for the toxicity of DDT crystals on a leaf surface was obtained by spraying a range of six concentrations of suspension on dock leaves on the day when toxicities were assessed; for this purpose, leaves detached from the plants were used. The kills recorded and the results of the chemical assays, as percentages of the original deposit remaining after correcting for leaf growth, are given in Tables IV and V, respectively. In some cases, no analytical figure was obtained for the rate of deposit sprayed; the result is then expressed as a percentage of the intended rate of deposit, and the figure in the Table is enclosed in brackets.

TABLE IV.

Toxicity after four periods of time of DDT deposits on leaves of plants and on glass plates kept in a greenhouse at 10°–21°C. Results are given as percentage kills of adult *T. castaneum.*

Nature of surface	Approximate initial deposit, microgm. per sq. cm.	Age of deposits in days 0	6	24	37
Plates	2	30	49	76	15
	4	93	100	100	93
	8	100	100	100	100
Dock	2	94	93	15	*
	4	100	100	100	89
	8	100	100	100	100
Cabbage	2	—	100	93	*
	4	—	100	100	*
	8	—	100	100	100
Marrow	2	—	100	51	61
	4	—	100	*	*
	8	—	100	100	100

* Represents leaves which died before assessment.

The biological results (Table IV) show little loss of toxicity, many of the kills being 100 per cent. even after 37 days; they are not very informative because, as a greater loss was expected when the experiment was planned, higher concentrations than were necessary were sprayed. The kills have not been corrected to allow for leaf growth, which was small in this experiment. The initial deposit values given in Table IV are only approximate, as the exact figures, known from the results of the chemical analyses of plates sprayed alongside the leaves and used in calculating the percentages, are different for each leaf owing to the unavoidable variations in spray deposit from one spraying to another.

TABLE V.

Percentage of DDT deposits remaining after three periods of time on foliage and glass plates kept in a greenhouse at 10°–21°C. Percentage as determined by chemical analysis, after correcting for leaf growth.

Nature of surface	Approximate initial deposit, microgm. per sq. cm.	Age of deposits in days		
		6	24	37
Plates	2	103	81	64
	4	98	86	73
	8	112	93	—
Dock	2	126	85	—
	4	131	112	(62)
	8	109	86	(100)
Cabbage	2	90	91	—
	4	100	81	—
	8	120	93	77
Marrow	2	—	73	(57)
	4	133	—	—
	8	147	95	—

(The dashes represent samples lost before or during analysis. The figures in brackets are based on approximate initial rates of deposit.)

The chemical results (Table V) show a slow decline in the rate of deposit, though in most cases more than half the DDT is still recoverable after 37 days. The recoveries on marrow and dock after six days' storage are very high. With marrow leaves there may be a tendency for the deposit on the leaf to be higher than on a plate sprayed at the same time, as the leaf hairs might assist impaction of the finer droplets.

Where the mortality figure was not 100 per cent., it was possible to use this figure to calculate the equivalent rate of deposit of DDT; this rate was read off the probit line constructed from the mortalities recorded on the surfaces that were sprayed to provide reference levels of toxicity. In Table VI are shown the figures obtained in this way, together with the rates of deposit found by chemical analysis after exposure of the surfaces for the same periods of time. This enables a direct comparison to be made between the actual amount of DDT present at various stages of a test, and its toxicity.

The agreement between chemical and biological results for the six figures obtained from leaf surfaces is reasonably good, the averages, in microgm. per sq. cm., being: chemical assay, 1·59; bioassay, 1·62. On plates, however, the deposits appear to be more toxic than would be expected from the DDT found (averages in microgm. per sq. cm.: chemical assay, 1·8; bioassay, 2·78). This supports a conclusion reached in a previous paper (Burt & Ward, 1955) that deposits on glass plates increase in toxicity when stored at 18°C.

TABLE VI.

Chemical and biological assays of rates of deposit of DDT on foliage and glass plates exposed in the greenhouse at 10°–21°C.

Nature of surface	Period of exposure in days	Approximate initial rate of deposit, microgm. per sq. cm.	Rate by chem. assay, microgm. per sq. cm.	Rate by bioassay, microgm. per sq. cm.
Dock	37	4	2·4	1·8
Marrow	37	2	1·14	1·5
Cabbage ..	24	2	1·40	2·0
Dock	24	2	1·02	1·1
Marrow	24	2	1·20	1·4
Dock	6	2	2·4	1·9
Plates	37	2	1·22	1·7
,, ...	37	4	2·7	3·9
,, ...	24	2	1·33	3·0
,, ...	6	2	2·0	2·4

Loss of crystalline DDT at air temperatures of 15–35°C.

This experiment was similar to the previous one but a different temperature range was used and some minor changes were made. *Cineraria* was used in place of marrow as a hairy-leaved plant; the other plants were cabbage and dock. The plants were kept in a greenhouse, without artificial heat, and in consequence night temperatures sometimes sank to 15°C., but temperatures below that were very rare. The plants were only shaded from direct sunlight if they showed signs of wilting; consequently, the leaves were often at a higher temperature than that of the air of the greenhouse, which sometimes reached 35°C.

Some difficulty was encountered because the plants grew rapidly in summer conditions, causing the leaves to reach maturity and wither quickly. This was especially so with cabbages and the trouble was partially met by nipping out the growing shoots of these plants. For each period of ageing, plant species and rate of deposit, two leaves were sprayed, so as to provide duplicates for comparison wherever possible and to reduce the loss of data due to death of individual leaves. Even so, the longest period for which we were able to keep a reasonably complete set of leaves was 30 days, although some glass plates were exposed for 50 days. Table VII shows the kills recorded on the surfaces after the various exposure periods.

In general, a deposit of 2 microgm. per sq. cm. has lost its toxicity after 16 days, while a deposit of 4 microgm. per sq. cm. remains toxic at 16 days, but has lost most of its toxicity by 30 days. The dock results are somewhat anomalous, as there appears to be no significant difference between 16 and 30 days. In Table VII, however, no account is taken of leaf growth, nor of the unavoidable differences in the original rates of deposit due to variations in the spraying process. The original rates of deposit, however, are known from the analyses of plates sprayed alongside the leaves. In Tables VIII and IX, the mortalities have been converted into equivalent rates of deposit, which have been expressed as percentages of the initial rates of deposit, after allowing for the effect of leaf growth. The conversion is carried out by reading off the rates of deposit equivalent to the observed mortalities on the dosage-mortality curves obtained at 0 days. The results of the chemical assays, recorded as percentages of the initial deposits, are also reported. Where kills of 100 per cent. or 0 per cent. were recorded, they have been calculated as kills of 95 per cent. or 5 per cent. and are preceded by " greater than " or " less than " signs, respectively.

TABLE VII.

Toxicity of DDT deposits after four periods of time, on foliage and on glass plates kept in a greenhouse at temperatures ranging from 15°–35°C. Results are percentage kills of adult *T. castaneum.*

Nature of surface	Approximate initial deposit, microgm. per sq. cm.	Age of deposits in days 0	16	30
Plates	2	40	2	0
	4	76	37	2
	8	96	95	84
Dock	2	84	13	26
	4	97	60	69
	8	100	100	97
Cineraria	2	85	3	0
	4	98	70	11
	8	100	97	100
Cabbage	2	91	0	2
	4	99	44	0
	8	100	98	33

Taking into account both the biological and chemical results presented in Table VIII, with dock there is little difference between the percentage of DDT lost after 16 days' and after 30 days' exposure; after each, the reduction in toxicity is of the order of 50 per cent. With *Cineraria* there is a greater loss at 30 days than at 16 days; the percentage lost from both dock and *Cineraria* after 16 days is similar. On cabbage there is a greater loss at both periods, and the difference between 16 and 30 days is more obvious.

It is possible that these apparent differences between leaf surfaces were really due to environmental effects, for, if the experimental period is divided into three periods of approximately a fortnight each, during the first fortnight when only the 30-day dock and *Cineraria* leaves were exposed, there was only one day with an outside air-temperature maximum above 70°F. During the second fortnight, when there were five such days, all the leaves except the 16-day cabbage were exposed; most of the loss from dock and *Cineraria* probably occurred in this fortnight. In the third fortnight, when all the cabbage leaves were exposed, there were eleven days above 70°F., five being above 80°F.; this might account for the losses from cabbage being greater than those from the other leaf surfaces.

On leaves, there are no consistent differences between chemical and biological losses. On plates (Table IX), however, the chemical estimations show a rapid loss of DDT from the plates sprayed with the two lowest rates of deposit, only 3 per cent. and 5 per cent. being left after 23 days' exposure during the hottest period of the experiment. The loss of biological activity, on the other hand, does not correspond with the loss of DDT as determined chemically but is much less. The activity of deposit rates of 2 and 4 microgm. per sq. cm., even after 45 days' exposure, had fallen only to 12 and 45 per cent., respectively, of the original values. This exaggeration of the toxicity of deposits on plates which

TABLE VIII.

Percentages of DDT deposits remaining on leaves grown in a greenhouse at 15°–35°C. Results have been corrected for growth of the leaves.

Type of leaf	Approx. initial deposit, microgm. per sq. cm.	By chemical assay after		By bioassay after	
		16 days	30 days	16 days	30 days
Dock	2	62	—	40, 28	19, 40
	4	40	49	71, 54	19, >92
	8	36	76	>61, >61	68, >60
Cineraria ..	2	34	36	21, <28	<25, <16
	4	69	76	48, 107	7, —
	8	76	50	52, >76	>36, —
Cabbage	2	25	6	<17, <16	26, —
	4	46, 42	14, 10	31, 19	<12, <16
	8	56	12, 47	47, —	12, 23
Mean ..	2	40	21		
	4	51	46		
	8	56	52		

Dashes represent leaves which died during exposure.

TABLE IX.

Percentage of DDT deposits remaining on glass plates exposed in a greenhouse at 15°–35°C., determined chemically and biologically.

Nominal initial deposit, microgm. per sq. cm.	By chemical assay after			By bioassay after		
	23 days	36 days	50 days	16 days	30 days	45 days
2	3	0	Tr., Tr.	42	<49, <31	12
4	5	3, 2	1, 1	79	15, <22	45
8	47	38, 46	27, 61	120	57, 83	20

Tr. = trace.

TABLE X.

Loss of DDT from leaves sprayed with suspension and emulsion. Percentage of DDT remaining and mortalities of adult *T. castaneum* on leaves immediately after spraying and after two periods of exposure in the greenhouse at 10°C.–21°C.

(a) leaves sprayed with DDT suspension

Days exposed	Rate originally applied, microgm. per sq. cm. (determined chemically)	Rate after exposure, microgm. per sq. cm. (determined chemically)	% increase in area of leaves on which rate after exposure was determined chemically	% DDT remaining (after correction for leaf growth)	% increase in area of leaves whose toxicity to *T. castaneum* after exposure was determined	Mortality of *T. castaneum* %
0	3·42	—	—	—	—	61
0	1·86	—	—	—	—	45
7	2·01	1·83	0	91	0	68
28	1·15	—	—	—	0	2
0	0·95	—	—	—	—	17
7	0·97	0·70	0	72	0	0
28	0·74	0·12	0	16	14	2
0	0·54	—	—	—	—	3
7	0·45	0·17	0	38	0	2
28	0·33	—	—	—	—	—
0	0·25	—	—	—	—	0
7	0·20	—	—	—	0	0
28	0·11	—	—	—	29	0

(b) Leaves sprayed with DDT emulsion

Days exposed	Rate originally applied, microgm. per sq. cm. (determined chemically)	Rate after exposure, microgm. per sq. cm. (determined chemically)	% increase in area of leaves on which rate after exposure was determined chemically	% DDT remaining (after correction for leaf growth)	% increase in area of leaves whose toxicity to *T. castaneum* after exposure was determined	Mortality of *T. castaneum* %
0	3·80	—	—	—	—	100
7	3·55	2·40	29	87	10	87
28	4·01	0·81	50	30	50	16
0	2·17	—	—	—	—	92
7	1·48	0·91	0	61	0	17
28	1·70	0·64	0	38	34	0
0	1·01	—	—	—	—	20
7	0·68	0·05	0	7	0	3
28	0·95	—	—	—	20	0
0	0·43	—	—	—	—	5
7	0·33	—	—	—	0	0
28	0·37	0·01	0	3	—	—
0	0·18	—		—	—	13

have been exposed and which have lost DDT was also found in the previous experiment, and it remains to be explained.

The differences in rates of loss from leaves and plates may be due to unequal heating of the two surfaces by the sun. The plates were exposed lying on their backs on the greenhouse staging. They were in sunlight whenever the sun was unobscured, whereas the leaves were frequently shaded by other leaves or were parallel with the sun's rays, and so not irradiated; the plates could only lose heat from their upper surfaces, while the leaves were cooled by the air on both sides. For these reasons, the plates were on the average considerably hotter than the leaves.

The chemical results on plates given in Table IX show that deposits at high rates are relatively much more persistent than those at lower rates. This is thought to be due to the ease with which the air near the plates becomes saturated with DDT. The rate of evaporation is thus largely determined by the amount of ventilation, so that under given conditions the amount of DDT lost will be to a large extent independent of the amount of DDT constituting the deposit.

Comparative Rates of Loss of Deposits of DDT from two Formulations.

In order to obtain some information on the relative persistence of two DDT formulations on leaf and glass surfaces, a further experiment similar to the two previous ones, except for certain differences described below, was carried out. The temperature range to which the surfaces were exposed was 10–21°C.

Two formulations were used, the suspension used in previous experiments, and an emulsion; their preparation is described above (p. 851). The various concentrations of DDT emulsion required were prepared in such a way that the DDT:xylene ratio was constant, whatever the final concentration of DDT in the spray mixture.

The amount of DDT present was estimated chemically, and its activity was estimated biologically initially, and after periods of one week and four weeks. Like the two previous experiments, this experiment was so designed that all biological assays took place on the same day. Only one species of plant was used; this limitation permitted a greater range of deposit densities to be sprayed and tested. Four concentrations were sprayed for each formulation, the rates being chosen after a preliminary experiment to determine the initial toxicities of the two formulations on the two surfaces, leaf and glass, respectively.

The percentage kills are presented in Tables X and XI, together with the initial rates of deposit and the percentage increases in area of the leaves due to their growth. The raw data are not very informative: as there is considerable variation in both the initial rates and the amounts of leaf growth, some sort of mathematical digestion is necessary before the figures for kill can be made comparable. The method of calculation used in the previous experiment was unsuitable in this case; too many of the kills recorded were very high or very low and consequently, when converted into equivalent rates of deposit, could only be expressed as "less than" or "more than" a particular figure. This resulted in a Table which was both confusing and misleading. The following procedure was therefore adopted:—

The percentage kills produced by unexposed deposits (0 days old) were converted to probits and plotted against the logarithms of their corresponding deposit rates, and a line relating kill to deposit rate was constructed. A similar line was constructed to relate to their corresponding initial deposit rates the kills produced on deposits which had been exposed 7 days. A correction was made for leaf growth, where necessary, by dividing the initial rates of deposit by the number of times by which the leaf had increased in area. Provisional probit lines only were constructed, since the numbers of significant points were too small to justify full probit transformations.

By using these lines it was possible to compare the toxicities of deposits of any given initial dosage rate (within the range used) both initially and after exposure for 7 days. Unfortunately, probit lines could not be constructed for deposits exposed for 28 days, as there were insufficient significant points. Hence, comparison between the toxicities of deposits exposed for 28 days and those exposed for 0 and 7 days could only be made at the rates of initial deposit actually applied to the surfaces which were to be exposed for 28 days.

These initial rates were therefore corrected for leaf growth and the kills corresponding to these rates were read off on the 0- and 7-day probit lines. In this way, a set of figures for kills after 0, 7 and 28 days was obtained, each figure

TABLE XI.

Loss of DDT from glass plates sprayed with suspension and emulsion. Percentage of DDT remaining and mortalities of *T. castaneum* on plates immediately after spraying and after two periods of exposure in the greenhouse at 10°C.–21°C.

(a) Plates sprayed with DDT suspension

Days exposed	Rate originally applied, microgm. per sq. cm. (determined chemically)	Rate after exposure, microgm. per sq. cm. (determined chemically)	% DDT remaining	Mortality of *T. castaneum* %
0	3·42	—	—	80
0	1·86	—	—	45
7	2·01	1·25	62	79
28	1·15	0·37	32	4
0	0·95	—	—	5
7	0·97	0·36	37	9
28	0·74	0	0	0
0	0·54	—	—	3
7	0·45	0·14	31	12
28	0·33	0	0	0
0	0·25	—	—	3
7	0·20	0	0	0
28	0·11	0	0	0

(b) Plates sprayed with DDT emulsion

Days exposed	Rate originally applied, microgm. per sq. cm. (determined chemically)	Rate after exposure, microgm. per sq. cm. (determined chemically)	% DDT remaining	Mortality of *T. castaneum* %
0	3·80	—	—	69
7	3·55	2·64	74	77
28	4·01	2·30	57	81
0	2·17	—	—	16
7	1·48	0·93	63	34
28	1·70	0·49	29	4
0	1·01	—	—	13
7	0·68	0·19	28	19
28	0·95	0	0	3
0	0·43	—	—	0
7	0·33	0·03	9	0
28	0·37	—	—	0
0	0·18	—	—	0

corresponding with the same initial rate of deposit. The sets of figures so obtained are shown plotted against periods of exposure in the lower halves of figs. 3 and 4. The points are joined by lines, which are labelled with the initial rates of deposit.

The results of the chemical analyses of the exposed surfaces are also given in Tables X and XI, expressed as percentages of the initial rate of deposit remaining after exposure.

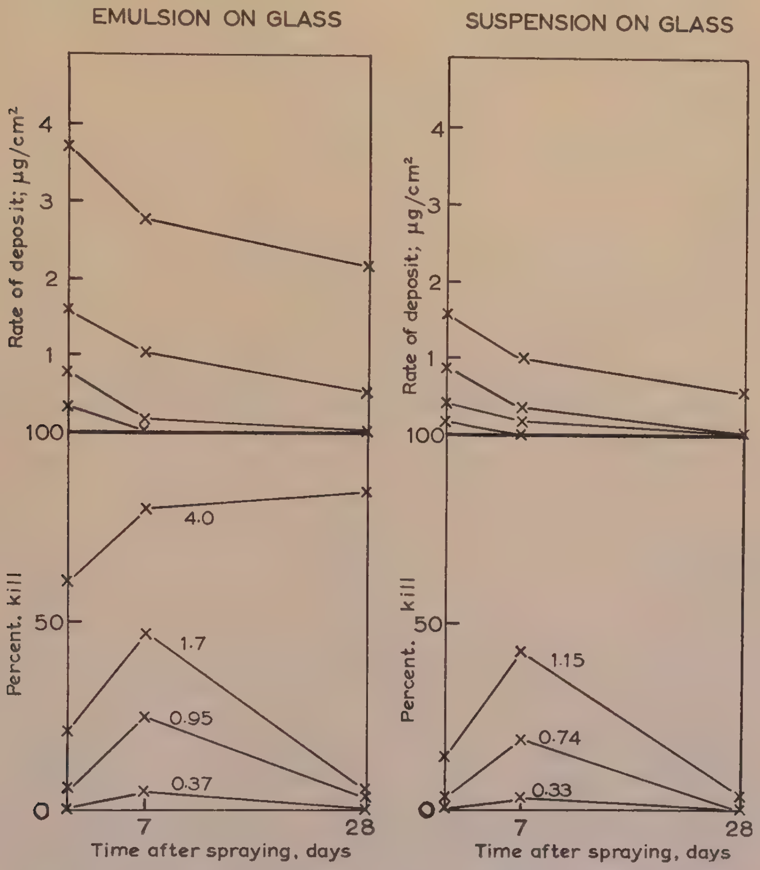


Fig. 3.—Upper sections:—Loss of DDT, as shown by chemical analysis, from emulsion- and suspension-deposits on glass plates exposed in a greenhouse at 10–21°C. Lower sections:—Effect of exposure of sprayed plates on their contact toxicity to *T. castaneum*. Rates of deposit before exposure, in microgm. per sq. cm., are indicated by numbers near the appropriate lines. Corrections have been applied to the results in both sections to allow for deviations from the intended values in the rates of deposit before exposure.

In the upper halves of figs. 3 and 4, the chemical results are plotted as microgm. per sq. cm. of DDT against period of exposure, so that the loss of DDT can be compared with the changes in toxicity. Before plotting the graphs, however, the figures for deposit density obtained by chemical analysis after exposure had also to be corrected for growth of the leaves and for the differences in the initial rates of deposit. The deposit before exposure (*i.e.*, the 0-day point on the graph) was taken as the mean of the initial rates of deposit on the two surfaces which were to be exposed for 7 days and for 28 days, respectively. The rates of deposit after exposure, as determined analytically, were corrected for leaf growth by multiplying them by the number of times by which the leaves had increased in area. They were then adjusted to the mean initial rates of deposit by multiplying them by the ratios of the mean to the actual initial rates of deposit.

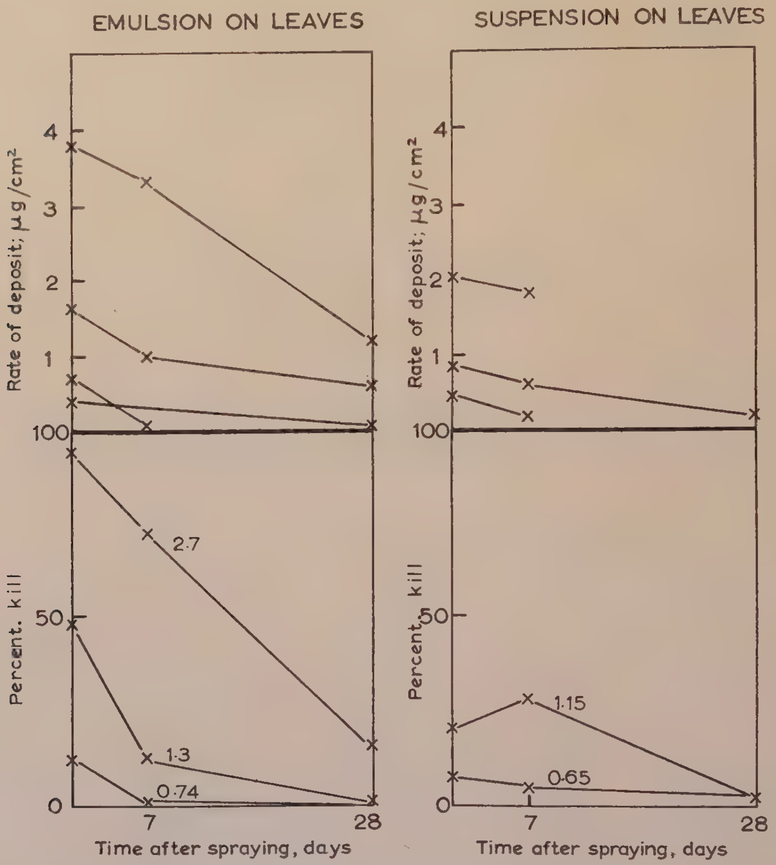


Fig. 4.—Upper sections:—Loss of DDT, as shown by chemical analysis, from emulsion- and suspension-deposits on leaves exposed in a greenhouse at 10–21°C. Lower sections:—Effect of exposure of sprayed leaves on their contact toxicity to *T. castaneum*. Rates of deposit before exposure, in microgm. per sq. cm., are indicated by numbers near the appropriate lines. Corrections have been applied to the results in both sections to eliminate the effect of leaf growth and to allow for deviations from the intended values in the rates of deposit before exposure.

The chemical results show that the rates of loss from plates and from leaves are of about the same order. This was to be expected as the experiment was conducted during the winter when there was little heating of the test surfaces by irradiation, and consequently both leaves and plates were approximately at air temperature. The deposits from suspensions persist rather longer than those from emulsions (see Table XI), possibly because the emulsion forms crystals which appear under the microscope to be somewhat thinner than the suspension crystals. The toxicity, at the 50 per cent. level, of deposits before exposure was rather greater for emulsion on leaves than for either emulsion on plates or suspension on leaves or plates. On plates the deposits from both formulations increased in toxicity after 7 days' exposure, despite loss due to evaporation, as shown in figs. 3 and 4. This effect had been observed with suspension-deposits in the previous experiments. Emulsion-deposits on leaves (fig. 4) declined in toxicity after both periods of exposure and at all rates of deposit. At the highest rate, the suspension-deposits on leaves showed an increase in toxicity after seven days, but the probit line for this period of exposure was unsatisfactory, and the apparent increase is probably due to a sampling error. Deposits on leaves or on wax-coated glass plates have not previously been found to increase in toxicity on storing.

The experiment showed that in general the emulsion-deposits behaved similarly, with regard to changes in toxicity and loss of DDT on exposure, to the deposits from suspensions which had been used in the earlier work.

Discussion.

Previous work relating temperature with loss of activity of persistent insecticides (Burgess & Sweetman, 1949; Teotia & Dahm, 1950; Mistric & Gaines, 1953; Burt & Ward, 1955) suggests that high temperatures may materially accelerate the rate of loss of DDT when it is applied as an insecticide to a variety of surfaces. Decker, Weinman & Bann (1950) concluded that there is a positive correlation between the vapour pressures of insecticides and their rates of loss from crops, which also suggests a connection between temperature and rate of loss of activity.

Our experiments confirm that temperature has a marked effect on the rate of loss of activity of DDT deposits. In both the experiments carried out in the temperature range 10°–21°C., little loss either of DDT or of biological activity had occurred at the higher dosage rates until the surfaces had been exposed for 28 days; at 24 days the loss was not yet very marked. At lower rates, though loss of DDT and of activity was small at 7 days, it was already appreciable at 24 days. On the other hand, when deposits were exposed in the range 15°–35°C., even at the highest dosage rates both the amount of DDT present and its biological activity had been halved after 16 days, and such variations as there were in the experimental results obtained were usually associated with variations in the temperatures to which the deposits were exposed.

Losses of DDT from plates exposed alongside plants were usually considerably greater than losses from foliage since, in sunshine, though the leaves were often shaded, the plates were constantly irradiated and so reached higher temperatures. The greater losses from deposits on plates were therefore to be expected and comparison of rates of loss from plates and from leaves could not be used to decide whether any of the loss was due to penetration of DDT into the foliage—another possible source of loss about which information was sought in these experiments.

It has been shown (Burt & Ward, 1955) that deposits of DDT crystals on glass surfaces increase in toxicity during storage at a temperature at which evaporation is negligible. The reason for this is unknown; it may be due to some change in the wetting agent which decreases the adhesion of the crystals to the glass. The increase was not observed when the DDT crystals were deposited on glass plates coated with cabbage wax and, since it was also shown that under the conditions of the experiment no appreciable penetration of DDT into the wax layer occurred, loss of DDT in this way could not have concealed an increase in the toxicity of the deposit. If, in the experiments described in this paper, the biological action of previously exposed plate- and leaf-surfaces bearing DDT deposits is compared with the amount of DDT remaining on similarly exposed surfaces, it is found that the toxicity per unit of DDT increases on plates but remains constant on leaves. Provided, therefore, that deposits on leaves, like deposits on wax-coated glass plates, do not increase in toxicity during exposure, it seems that, with the formulations used, loss of DDT due to its penetration into foliage is not sufficient to be detected by the method of bioassay used.

In general, this conclusion is in agreement with previous work. Martin & Batt (1954), however (in work published after this paper was originally drafted), have found that apple foliage sprayed with DDT emulsion or suspension retains about 15 per cent. of the DDT in such a way that it cannot be removed by washing with carbon tetrachloride. This internal DDT persisted even when most of the external deposit had been lost by weathering for 70 days. These authors found similar evidence for penetration into potato foliage, and Satyanarayana (1954) gives somewhat similar evidence for penetration into apple foliage. We have repeated the experiment of Martin & Batt, using cabbage leaves and following our own procedure (p. 850) for removing the superficial DDT. We, too, have found that the washed leaves contain DDT which can only be recovered by drying and extracting with solvent. About a fortnight after applying a crystalline suspension of DDT to the leaves at a rate of 4 microgm. per sq. cm., the "internal" DDT rose to a maximum value of about 10 per cent. of the amount originally sprayed. Thereafter, it remained constant while the external deposit declined. These findings are broadly in agreement with those of Martin & Batt. The proportion of insecticide lost by penetration in this way is not, therefore, sufficient to cause a serious reduction in the toxicity of the deposit. Other workers have found substantial absorption of DDT into foliage after spraying with a solution in a volatile solvent (Gunther, Lindgren, Elliott & LaDue, 1946), or in an oil (Stafford & Hinkley, 1946; Symes, Hadaway, Barlow & Galley, 1948; Hadaway & Barlow, 1949); no other workers using suspensions or emulsions have found any substantial absorption.

In our experiments some possible sources of loss of toxicity which might be present under field conditions were excluded: the glass of the greenhouse, in which the plants were kept, screened the deposits from some of the ultra-violet radiation of sunlight; leaf growth was measured and the results were corrected accordingly; washing of the leaves by rain could not occur. Thus, all the losses observed were due to evaporation or decomposition of the insecticide, and they were sufficiently great to be of practical importance. Losses were proportionately greater for light deposits than for heavy ones, probably because the rate of evaporation is limited by the saturation of the air near to the deposit. At similar temperatures under conditions of free ventilation the rate of evaporation might be much greater; at much higher rates, however, such as those used when spraying the walls of houses to control flies and mosquitos (generally 100–500 microgm. per sq. cm., as compared with 0·1–10 microgm. per sq. cm. used in our work), the proportion of deposit lost by evaporation in the course of a few weeks would probably be negligible.

Where maximum persistence is required, and where conditions favour loss by evaporation, a residual insecticide should evidently be applied at the maximum economic rate. Where a choice exists between a cheap insecticide of low activity and a relatively expensive one which has a similar vapour pressure but is much more active, maximum persistence might be obtained at lower cost by applying the cheaper insecticide at a high rate rather than by using the more active one at a lower rate.

Summary.

A method is described of applying even deposits of insecticide to leaves without detaching the leaves from the plants. The insecticide is sprayed by hand

from an air-operated paint-spray gun under controlled conditions. Using this method for applying the insecticide, the persistence of DDT on living leaves and on glass plates was investigated.

The DDT content of the deposits was estimated chemically by the Schechter-Haller method of analysis and the toxicity of the deposits was measured by allowing adult *Tribolium castaneum* (Hbst.), confined within glass collars, to crawl on the surfaces to be tested. The deposits were found to be more toxic on leaves than on plates. This difference was shown to be due in part to the greater humidity of the environment during exposure of the test insects to deposits on leaves, as a similar enhancement of toxicity occurred when, during exposure of insects to deposits on glass or Cellophane, the humidity was kept at a higher level than usual.

The rate of loss of toxicity and of DDT when deposits were exposed to sunlight in a greenhouse for varying periods within two different ranges of air temperature was studied. The deposits were derived either from emulsions or crystalline suspensions. At the lower range of air temperatures (10°–21°C.) there was a loss, after 37 days, of about one-third of the DDT from suspension-deposits applied at the rate of 2 microgm. per sq. cm. to either leaves or plates. For deposits on leaves, the losses of DDT indicated by bioassay were about equal to those found by analysis, but for deposits on plates the toxicity after exposure was markedly greater than was to be expected from the amount of DDT remaining. In another experiment within the same temperature range, but with lower rates of deposit, loss of DDT occurred more rapidly, the lower the rate of deposit, the greater being the percentage of DDT lost. Deposits from DDT emulsions, included in this experiment, behaved similarly to suspension-deposits.

Suspensions only were used with the higher range of air temperatures (15–35°C.), at deposit rates of 2–8 microgm. per sq. cm. Deposits were lost more rapidly from plates laid on a greenhouse bench than from living leaves, probably because the plates, as a result of insolation, were at a higher average temperature. Again, the lower the rate of deposit the greater was the percentage lost, and the biological activity of the exposed plates, but not of the leaves, was greater than was to be expected from the amount of DDT remaining.

It is concluded that the main cause of loss of p,p′DDT from crystalline deposits of the pure material exposed to sunlight in a greenhouse is the volatility of the DDT. Since the lower the rate at which the DDT is applied, the greater is the percentage lost in a given time, it is suggested that where maximum persistence of an insecticide is required, and conditions favour loss by evaporation, the insecticide should be applied at the maximum rate practicable.

Loss of toxicity resulting from penetration of DDT into the leaf was too small to be of practical importance.

Acknowledgement.

This work was financed by a grant from the Colonial Insecticides Committee; we wish to thank the committee for permission to publish this paper.

References.

Bliss, C. I. (1934). The method of probits.—Science, **79**, pp. 38–39, 409–410.

Burgess, A. F. & Sweetman, H. L. (1949). The residual property of DDT as influenced by temperature and moisture.—J. econ. Ent., **42**, pp. 420–423.

Burt, P. E. & Ward, J. (1955). The persistence and fate of DDT on foliage. I. The influence of plant wax on the toxicity and persistence of deposits of DDT crystals.—Bull. ent. Res., **46,** pp. 39–56.

Decker, G. C., Weinman, C. J. & Bann, J. M. (1950). A preliminary report on the rate of insecticide residue loss from treated plants.—J. econ. Ent., **43,** pp. 919–927.

Finney, D. J. (1947). Probit analysis.—256 pp. Cambridge, Univ. Press.

Gunther, F. A., Lindgren, D. L., Elliot, M. I. & LaDue, J. P. (1946). Persistence of certain DDT deposits under field conditions.—J. econ. Ent., **39,** pp. 624–627.

Hadaway, A. B. & Barlow, F. (1949). Further studies on the loss of insecticides by absorption into mud and vegetation.—Bull. ent. Res., **40,** pp. 323–343.

McIntosh, A. H. (1947). Relation between particle size and shape of insecticidal suspensions and their contact toxicity. I. D.D.T. suspensions against *Tribolium castaneum* Hb.—Ann. appl. Biol., **34,** pp. 586–610.

Martin, J. T. & Batt, R. F. (1954). Spray application problems: VII. The determination of DDT in plant materials.—Rep. agric. hort. Res. Sta. Bristol, 1953, pp. 121–128.

Mistric *jr.*, W. J. & Gaines, J. C. (1953). Effect of wind and other factors on the toxicity of certain insecticides.—J. econ. Ent., **46,** pp. 341–349.

Pradhan, S. (1949*a*). Studies on the toxicity of insecticide films. II. Effect of temperature on the toxicity of DDT films.—Bull. ent. Res., **40,** pp. 239–265.

Pradhan, S. (1949*b*). Studies on the toxicity of insecticide films. III. Effect of relative humidity on the toxicity of films. Bull. ent. Res., **40,** pp. 431–444.

Satyanarayana, P. (1954). The insecticidal efficiency of DDT deposits applied to apple foliage as solutions or emulsions.—J. hort. Sci., **29,** pp. 112–125.

Stafford, E. M. & Hinkley, H. S. (1946). DDT and related compounds for control of Black Scale on olives.—Circ. Calif. agric. Exp. Sta., no. 365, pp. 91–93.

Symes, C. B., Hadaway, A. B., Barlow, F. & Galley, W. (1948). Field experiments with DDT and benzene hexachloride against Tsetse (*Glossina palpalis*).—Bull. ent. Res., **38,** pp. 591–612.

Teotia, T. P. S. & Dahm, P. A. (1950). The effect of temperature, humidity and weathering on the residual toxicities to the House Fly of five organic insecticides.—J. econ. Ent., **43,** pp. 864–876.

THE DEVELOPMENT AND FECUNDITY OF THE ORIENTAL FRUIT MOTH, *GRAPHOLITHA (CYDIA) MOLESTA* (BUSCK) UNDER CONTROLLED TEMPERATURES AND HUMIDITIES.*

By Ghulam-Ullah Chaudhry

Contents.

	Page
Technique and Methods ...	870
Development and Viability ...	871
Egg stage ...	872
Larval stage ...	877
Pupal stage ...	879
Larval diapause ...	883
Short diapause ...	883
Long diapause ...	884
Emergence under different conditions ...	887
Fecundity under different Conditions ...	888
Effect of temperature and humidity on fecundity ...	888
Meteorological Data and Incidence ...	891
Summary and Conclusions ...	894
Acknowledgements ...	896
References ...	897

Grapholitha (*Cydia*) *molesta* was described by August Busck of the United States Bureau of Entomology under the name *Laspeyresia molesta* (Quaintance & Wood, 1916). Prior to this, Froggatt (1914) mentioned the insect as an unidentified enemy of peach in Australia under the popular name, Peach Tip Moth. Enquiries made by Haeussler (1940) in Japan revealed that it was known in Japan in 1901 and 1902, especially as a pest of sand pear.

The pest has been known under several common names in the past, *e.g.*, Peach Tip Moth, Smaller Pear Borer, Oriental Peach Worm, Oriental Peach Moth and Oriental Fruit Moth. The last of these names has been adopted here.

The Oriental Fruit Moth is an important insect pest of peach and other stone fruits, apple, quince and pear. The larvae bore into tender shoots of peach, which is the major host-plant in the United States of America, and later they attack its fruits. In the case of other hosts the pest generally attacks fruits. The moth was reported first in 1916 doing considerable damage to peach trees within a radius of 20 miles around Washington, D.C. Subsequent investigations showed that it was introduced into that locality on flowering cherries imported from Japan about three years earlier. By 1918 the pest had spread to New Jersey, New York and Connecticut; it has been spreading to deciduous orchards in all directions ever since. In spite of strict quarantine measures the pest is now well established in California.

Outside the United States the Oriental Fruit Moth has been recorded from Canada, Italy, France, New Zealand, Australia, China and Japan. In

---

* This paper embodies material approved by the School of Graduate Studies of Michigan State College of Agriculture and Applied Science, East Lansing, Michigan, U.S.A., in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Japan, damage by it was first noticed in Okayama Prefecture in 1901 and 1902, as reported by Harukawa (1923) and Haeussler (1940). It is now generally distributed throughout the central and southern parts of Japan. Both fruits and twigs of peach, sand pear, pear, quince, apple, apricot and black plum are attacked but only the twigs in the case of cherry, Japanese flowering cherry, sand cherry, Japanese apricot and plum. In Japan, it is of primary importance as a pest of sand pear which is of more importance as a fruit crop than the peach.

So far the Oriental Fruit Moth is not reported from Pakistan and India, although two closely related species, the Codling Moth, *Carpocapsa* (*Cydia*) *pomonella* (L.) and the Peach Twig Borer, *Anarsia lineatella* Zell. are serious pests in the temperate fruit-growing areas of these countries. It is, of course, just possible that *G. molesta* has not yet been introduced to this region but it is more likely that climatic conditions are not altogether suitable for its development.

The biology and control of the pest have been studied extensively at different agricultural experiment stations in the United States, Canada and Japan. In almost all these investigations, the insects have been studied either in the field or under uncontrolled conditions in the laboratory. Hence it is not possible to evaluate the effect of various environmental factors. Comparatively little is known about the potentialities of the insect, the rate of its development, upper vital limits for the various stages and the fecundity and longevity of adults under different controlled conditions. Modern ecologists have tended to study insects only in the field. Accurate analysis of observations in the field is very difficult; in spite of the fact that varying temperatures in nature are more important from an ecological point of view, research at constant temperatures is of the utmost importance to a proper understanding of these variations. Laboratory and field ecology are interdependent and both are essential. By correlating the results of study in the laboratory with those in the field it is sometimes possible to solve problems of insect abundance. Uvarov (1931) emphasised the importance of properly planned studies in the laboratory so as to utilise the results in understanding the problems in nature.

Control of the Oriental Fruit Moth has depended to a large extent in the past on parasites. In order to assess the potentialities of a pest and its parasites properly, a knowledge of their behaviour under different controlled conditions of environment is of fundamental importance. Such studies would reveal the optimum conditions for both the pest and its parasites.

Temperature is the greatest single factor affecting the geographic distribution of any species of insect. The biotic potential, its behaviour, form and structure, are all influenced by this environmental factor. Apart from its direct effects, temperature influences other factors, such as light, moisture, movement of air, etc. The distribution of animals in many parts of the world is more or less closely linked with temperature. Another factor which controls the geographic range of an organism is moisture.

With these points in view, investigations on the ecology of the Oriental Fruit Moth were started in 1950 at East Lansing, Michigan (U.S.A.), by rearing the insect under constant temperatures and relative humidities. Meteorological data from three typical stations in the United States have also been compared with those from three typical peach- and apple-growing areas in Pakistan, in order to examine the possibilities of the pest establishing itself in the latter country.

Technique and Methods.

About a dozen hibernating larvae of the Oriental Fruit Moth were received from Benton Harbour, Michigan, in January–February 1950. During May 1950 several visits were made to the area, and quince and peach trunks were examined for hibernating larvae and pupae but very few specimens were collected. In all, about two dozen moths emerged and these died after laying only five eggs.

Owing to extended cold weather, the pest did not make its presence noticeable in the Lansing area till about the end of June 1950. Peach orchards around Lansing, Mason and Grand Rapids were examined frequently from June to September 1950 and the infestation in twigs of peach was never found to be more than 0·1 per cent., although on some individual trees it would range from 2 to 5 infested shoots. Wilted shoots with the larvae boring inside were cut and brought to the laboratory.

The cut shoots were kept standing in moist sand and this generally allowed the larvae to become fully grown and leave the shoots to pupate in corrugated paper sheets provided for the purpose. The pupae were kept at room temperature (70 to 80°F.). The moths emerging from this material were liberated for oviposition in cages, 10″ × 10″ × 8″, made of wooden frames, the sides and tops of which were covered with thin muslin applied from inside. The cages were kept at room temperature over moist sand in large enamel trays. A wad of cotton-wool soaked in thin sugar solution was kept in each cage for the moths to feed upon. Fresh peach shoots were put in small bottles and tubes filled with water, and kept in the cages for oviposition, the bottles and tubes being wrapped in cloth to prevent the moths from laying eggs on the glass.

The shoots carrying eggs were removed from the cages every morning and, a few hours before the larvae were due to hatch, they were placed on partly sliced apples in glass dishes and beakers which were maintained at the temperature at which the larvae were to be reared. The larvae entered the apples soon after hatching and they would normally leave the fruit only after they were full-grown and ready to spin cocoons. The entire rearing in the laboratory was done on Jonathan apples removed from the trees in August and stored at 50°F. A known number of fully grown larvae were transferred to corrugated-paper strips in small glass vials, where they spun their cocoons and pupated. The mouth of each vial, which was kept at the required temperature and humidity, was covered with cloth to prevent the larvae from escaping.

The moths emerging from the vials were released in cages for oviposition. As these cages were to be kept in incubators they had to be smaller than those kept for general rearing at room temperature. They consisted of 6″ diameter wire loops supported by 8″ long pieces of wire; the sides and tops were covered with thin muslin and they were kept on moist sand in glass dishes. The moths were fed on sugar solution absorbed in cotton-wool. The eggs laid on the green peach shoots were counted daily and the shoots changed, a regular supply being available from seedlings raised in the greenhouse.

For 60° and 65°F., a refrigerating cabinet fitted with a special electric thermostatic control was used; for higher temperatures, electric incubators with accurate thermostatic controls were employed. The required temperatures did not fluctuate by more than 0·5°F.

Constant humidities in closed spaces can be obtained by using sulphuric-acid solutions or supersaturated-salt solutions; in these experiments salt solutions were used. This method has the advantage in that a standard solution is maintained which gives constant humidity; it does not require frequent changing and does not spoil easily. Chemically pure salts appropriate for each relative humidity at different temperatures were used (Hodgman, 1949). They were placed at the bottom of desiccators and just enough distilled water was added to cover the surface of the salt.

Development and Viability.

Following its discovery in the District of Columbia in 1916, the Oriental Fruit Moth was studied extensively at several agricultural experiment stations in the

United States. The first report on its life-history was published by Garman (1917), followed by that of Wood & Selkregg (1918). Stearns (1921) carried out extensive studies in an open-air insectary in northern Virginia. Stearns & Peterson (1928) studied the seasonal life-history in New Jersey, Snapp & Swingle (1929) in Georgia, Garman (1930) in Connecticut, Stearns & Neiswander (1930) in Ohio, Eddy & Nettles (1931) in South Carolina and Alden & Clarke (1931) in Georgia. In all these cases the investigators studied the insect either in the orchard or in the insectary.

Harukawa (1929) investigated the relation of temperatures to the growth of the moth in Japan. Peterson & Haeussler (1930) also studied some aspects of the life-history in relation to temperature, either that prevailing in the orchard or in the insectary. Dustan & Armstrong (1933), working in the Niagara Peninsula of Canada, made some observations to find out the effect of mean temperature and humidity in the insectary.

During the present investigation, the development and fecundity of the moth were studied in the laboratory under constant temperature and humidity conditions.

Egg Stage.

Effect of temperature on development.

(i) *Incubation period.*—The incubation period of the Oriental Fruit Moth has been studied by several workers in the past. Under insectary conditions Stearns (1921) and Stearns & Neiswander (1930), working in Ohio, recorded an incubation period of 4·4, 4·9, 6·05 and 9·4 days for the second, third, fourth and fifth broods, respectively, with a maximum of 17 days and a minimum of 3 days.

None of the previous workers studied the effect of humidity on the incubation period. The results obtained under constant temperatures and humidities in the present investigation are given in Table I and shown graphically in figs. 1 to 3. It will be seen that the incubation period decreased with rise of temperature until a minimum of 2·75 days was reached at 94°F., thereafter it began to increase. From these data it is clear that the eggs continue to develop at fairly high temperatures.

TABLE I.

The incubation period (days) of eggs under different conditions.

Temperature (°F.)	Relative humidity					
	100%		70%		35%	
	Incubation period	No. of observations	Incubation period	No. of observations	Incubation period	No. of observations
60	7·0	83	7·5	51	8·0	36
65	5·81	237	5·75	152	6·0	161
75	4·16	180	3·9	138	4·2	116
85	3·3	117	3·27	125	3·4	124
94	2·76	45	2·75	44	—	—
95	3·5	31	3·3	42	—	—

(ii) *Threshold of development.*—The relation of incubation period to temperature is shown in figs. 1 to 3. The reciprocals of the periods multiplied by one hundred (index of development) are also plotted. The theoretical threshold of development, as shown by the intersection of the lines of indices of development and the temperature axes lies between 40° and 44°F., depending upon the relative humidity prevailing at the time; it is least at 100 per cent. and highest at 35 per cent. R.H. Dustan & Armstrong (1933) reported an incubation period of 33·5 days

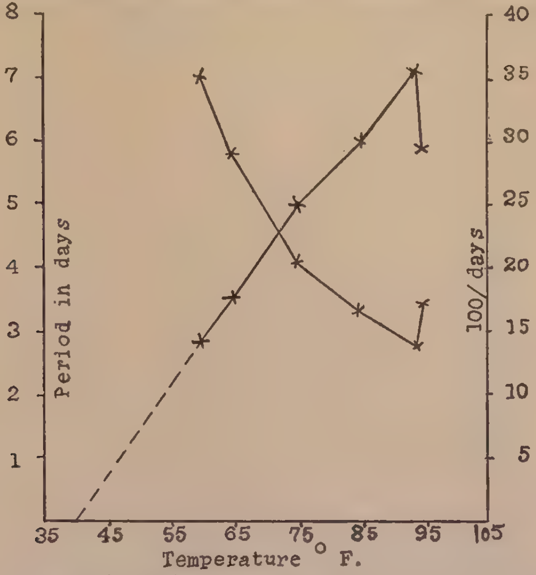


Fig. 1.—Incubation period of, and index of development for, eggs of *G. molesta* at constant temperatures and 100% relative humidity.

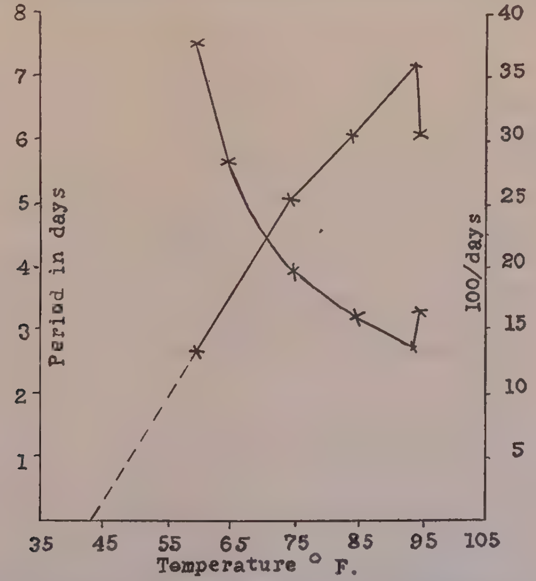


Fig. 2.—Incubation period of, and index of development for, eggs of *G. molesta* at constant temperatures and 70% relative humidity.

at an average daily temperature of 45·6°F. In autumn and spring, there being wide fluctuations in daily temperature, some development would occur at higher temperatures, whereas it would cease at lower temperatures, thereby considerably lengthening the incubation period. In the present investigations, eggs kept at 50·5°F. hatched in 24 and 25 days at 100 and 70 per cent. R.H., respectively. The graph drawn by Harukawa (1929) shows the threshold of development to be 10°C. (50°F.) which appears to be very high. Shelford (1927) gave 44° to 49°F. as the threshold of development for the Codling Moth, *Carpocapsa pomonella*, depending upon humidity, other weather factors, the generation and the individual. The eggs of the Oriental Fruit Moth can, therefore, develop at lower temperatures than those of the Codling Moth.

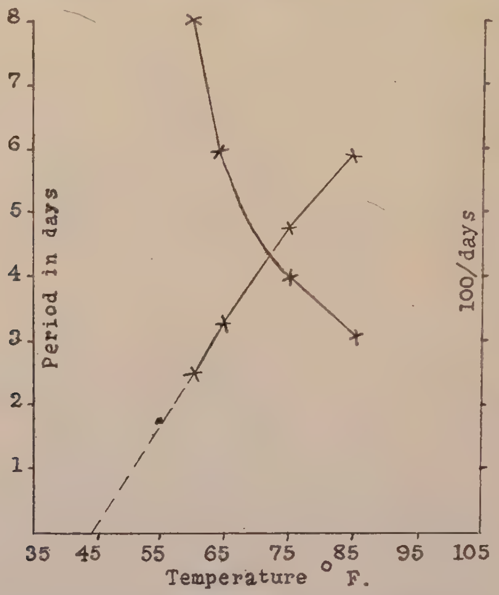


Fig. 3.—Incubation period of, and index of development for, eggs of *G. molesta* at constant temperatures and 35% relative humidity.

(iii) *Upper vital limit.*—The lines of indices of development in figs. 1 to 3 are fairly straight up to a temperature of 75°F. at each of the three relative humidities. After this they decline towards the right, indicating that although incubation is more rapid at temperatures above 75°F., the rate of development is not maintained uniformly. The bend is least at 70 per cent. R.H. and greatest at 35 per cent., showing the strong influence of humidity on the rate of development. Glenn (1922), in the case of *C. pomonella*, found 76°F. to be the temperature of maximum development, which is much the same as for the Oriental Fruit Moth.

The upper vital limit of the eggs of *G. molesta* is slightly above 95°F., probably 96°F., those kept at 95°F. failed to hatch at 35 per cent. R.H., although they hatched at higher humidities. Eggs kept at 98°F. for 48 hours did not hatch at any relative humidity but they were able to withstand short exposures to a temperature of 105°F. as shown in Table II. Eggs laid during the evening at a room temperature of 70° to 80°F. were exposed in the morning to temperatures of 98° and 105°F., for periods ranging from two hours upwards, and were then transferred to the room temperature. A portion of the eggs from each lot was kept as a check at room temperature. Examination of Table II shows that an

TABLE II.

Effect of short exposures to high temperature on the duration and viability of eggs.

Temp. (°F.)	Exposure (hrs.)	Relative humidity									Control	
		100%			70%			35%				
		No. of eggs exposed	No. of eggs hatched	Total incubation period (days)	No. of eggs exposed	No. of eggs hatched	Total incubation period (days)	No. of eggs exposed	No. of eggs hatched	Total incubation period (days)	% viability	Incubation period (days)
95	48	50	48	3·0	50	47	3·0	50	29	3·25	96	4·5
98	24	30	24	4·62	30	24	4·66	30	17	4·75	98	3·8
98	36	30	25	4·7	30	18	4·8	30	4	5·0	98	4·0
98	40	30	22	4·75	30	12	5·0	30	—	—	98	3·8
98	48	30	—	—	30	—	—	30	—	—	98	3·8
105	4	30	27	4·02	30	26	4·12	30	18	4·37	98	3·75
105	6	30	25	4·5	30	25	4·5	30	18	4·5	98	3·8
105	21	28	12	5·3	28	12	5·5	32	8	5·75	98	3·8

exposure of 48 hours to 98°F. was fatal. Exposures of less than 40 hours were not so harmful but the incubation period was significantly lengthened and usually ranged from 4·5 to 5·0 days as compared with 3·8 days for the control, showing that these exposures retarded or arrested development. Black spots, showing almost full development of the larvae inside egg shells appeared in the majority of cases even though actual hatching did not occur, indicating that some development had taken place even at 98°F. and that this temperature is slightly above the upper vital limits for the eggs. Eggs exposed for 21 hours to 105°F. hatched in 5·3 to 5·75 days, whilst those exposed for six hours took only 4·5 days to hatch. The viability of eggs exposed to 105°F. for 21 hours ranged from 43 per cent. at 100 per cent. R.H. to 25 per cent. at 35 per cent. R.H. In nature, even though the relative humidity of the air may be low, the eggs, being laid on green succulent leaves and shoots, may not suffer to any appreciable extent. Longer exposures at 105°F. would, however, affect the viability of the eggs very adversely and shorter exposures to temperatures above 105°F. may be equally harmful.

Effect of humidity on development.

The influence of humidity on the rate of development of eggs is given in Tables I and II. The rate is somewhat higher at 70 per cent. R.H. than at 100 per cent. R.H. at medium temperatures but the difference is not well-marked, especially at higher temperatures. Generally, eggs kept at 70 per cent. R.H. hatched a couple of hours before those at 35 per cent. and at about the same time as those kept under saturated conditions. These observations show that the shell does not easily allow loss of moisture from the egg. The flat and scale-like appearance of the eggs may be quite helpful in this respect. Furthermore, as the eggs are laid on the green and succulent tissues of the plant they are not likely to suffer from low atmospheric humidity.

Effect of temperature and humidity on viability.

The viability of eggs of *G. molesta* varies considerably under different conditions, particularly at adverse temperatures. Stearns & Neiswander (1930), in Ohio, found the viability of eggs to be 97·57, 98·2, 96·6 and 91·3 per cent. for the second, third, fourth and fifth brood, respectively.

TABLE III.

The viability of eggs under different conditions.

Temperature (°F.)	Relative humidity								
	100%			70%			35%		
	Total no. of eggs	No. of eggs hatched	% viability	Total no. of eggs	No. of eggs hatched	% viability	Total no. of eggs	No. of eggs hatched	% viability
60	92	83	90	68	51	75	50	36	72
65	256	237	92·5	196	152	77·5	208	161	77·4
75	183	180	98·3	140	138	98·6	132	116	87·8
85	120	117	97·5	128	125	97·5	160	124	77·5
94	50	45	90·0	50	44	88	50	0·0	0·0
95	90	31	34·0	80	42	52·5	60	0·0	0·0

Data on the viability of eggs obtained during the present investigations are given in Tables II and III. It is evident from these data that the eggs can tolerate fairly high temperatures and low humidities. At medium temperatures the viability was seldom less than 75 per cent., even at the lowest humidity. Near the upper vital limit, the deleterious effect of low humidity became markedly pronounced, as eggs at 35 per cent. R.H. failed to hatch at 94° and 95°F. Near-saturated relative humidities are, therefore, beneficial and drier conditions harmful. The influence of relative humidity seemed to be more marked on the viability of the eggs than on the incubation period.

Larval Stage.

Effect of temperature on development.

(i) *Duration.*—The larval period is here taken to mean the interval between eclosion from the egg and the commencement of spinning the cocoon, whether it be for immediate pupation or for the purpose of hibernation. The feeding period of the larvae varies considerably in nature depending upon the altitude, latitude and time of the year. The quantity, quality and kind of food have also been known to influence the length of this period and, apart from the above factors, there are large individual variations within any given lot of larvae kept under uniform conditions.

The larvae have been studied extensively in different parts of the United States but the duration of the larval period has usually been given according to the brood, reared in the insectary under uncontrolled conditions of temperature. Dickson (1950) studied the larvae under constant temperatures but did not mention the duration of the feeding period. Peterson & Haeussler (1930) found that late in the season in New Jersey, the overwintering larvae in particular required 50 to 115 days to become fully grown. At an average temperature of 65·5°F., Dustan & Armstrong (1933) working in Ontario, Canada, found the feeding period of the larvae to be 28 days when fed on stored apples and 20 days when supplied with peach shoots. In late autumn at an average temperature of 46·5°F., they found that some caterpillars required 80 to 92 days to become fully grown.

In the present investigation the larvae were fed on stored apples, and were reared at constant temperatures of 65°, 75°, 85° and 95°F. As the larvae always feed by boring into food saturated with moisture they could not be reared on semi-dry food. The results are given in Table IV and shown graphically in fig. 4.

TABLE IV.

The duration and viability of larval stage under different conditions.

Temperature (°F.)	Larval period in days			No. of larvae kept	No. of larvae which spun cocoons	Viability %
	Average	Maximum	Minimum			
65	36·81	58	22	7580	958	12·65
75	24·41	36	14	7706	1286	16·7
85	20·45	38	10	6429	1182	18·4
95	18·0	25	11	1538	228	14·8

They suggest that a constant temperature of 75°F. is very close to the optimum temperature for larval development, the optimum range probably terminating at 85°F. or even lower.

(ii) *Threshold of development.*—The relation of larval feeding period to temperature is shown in fig. 4. The reciprocals of the periods multiplied by one hundred (index of development) are also plotted. Harukawa (1929, fig. 3) gives the line of index of development as crossing the temperature axis at 10°C. (50°F.), which seems to be high. However, he himself was not sure of the accuracy of his experiments. This line, according to the present work, crosses the temperature axis at 43·5°F., but the actual threshold of development may lie a few degrees below that.

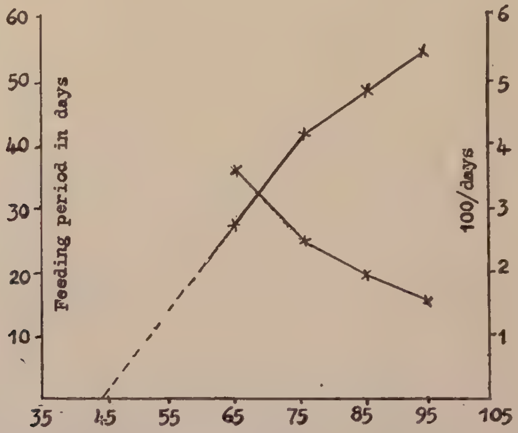


Fig. 4.—The feeding period of larvae in apples at constant temperatures and index of larval development of *G. molesta*.

Glenn (1922) and Shelford (1927) found 47·5°F. to be the theoretical threshold of development for the larvae of *Carpocapsa pomonella*. In calculating day degrees, they employed 50°F. as the starting point. Thus, larvae of the Oriental Fruit Moth can develop at temperatures lower than those for the larvae of *C. pomonella* and can continue to develop for a longer period in the late autumn. In nature, the larvae of *C. pomonella* go into hibernation much earlier than those of the Oriental Fruit Moth and this is probably one of the reasons for the smaller number of generations in the case of *C. pomonella* under similar conditions.

Effect of temperature on viability.

Information on the effect of temperature on larval viability is rather scanty. Harukawa's (1929) data based on a small number of individuals showed that there was 14 per cent. mortality at 20°C. (68°F.), 20·8 at 25°C. (77°F.), 12·6 at 27°C. (80·6°F.), 40 at 33°C. (91·4°F.) and 81·2 at 34°C. (93·2°F.). Stearns & Neiswander (1930) studied the effect of food on larval viability. They found that viability was 44, 33, 56·9, 12 and 13·3 per cent., respectively, when the larvae were fed on peach, plum, apple, pear and quince.

In the present experiments the larval viability as shown in Table IV was found to be 12·65, 16·7, 18·4 and 14·8 per cent. at 65°, 75°, 85° and 95°F., respectively. These figures are rather low, probably because they are based on the rearing of several thousand young larvae in small cages. Growth of fungus and free water accumulating from apples also reduced the number of larvae reaching maturity. In cases where a few individuals were reared the viability was sometimes as high as 50 to 70 per cent. In nature, mortality of larvae might be expected to be high on account of the unavailability of the right type of food at the proper time, driving rains, diseases, parasites, predators and other factors. Gummosis from the twigs and fruits of peach injured by larval borings is of common occurrence and not infrequently creates conditions unsuitable for the survival of the larvae feeding therein.

Pupal Stage.

The fully grown larvae leave the fruit in which they have fed and come to the top of the rearing dish to spin their cocoons. These larvae were removed every day from dishes kept at various constant temperatures, counted, and put in small glass vials containing short strips of corrugated paper where they would rapidly spin cocoons. The period between the commencement of spinning and pupation inside the cocoon is the prepupal period and several workers in the past have referred to this separately from the pupal period. This necessitates tearing the cocoon and disturbing the larvae, or the use of semi-transparent paper. For the present investigation it was not considered necessary to distinguish the prepupal period from the pupal period. Whenever the pupal period or pupal stage is mentioned below, it should be taken to mean the entire period from the time the larva started spinning a cocoon to its final emergence as a moth.

The pupae are considerably influenced by temperature and humidity, perhaps more so than the eggs. Stearns & Neiswander (1930), working in Ohio, found the pupal period to be 15·2, 16·7 and 16·5 days for the second, third and fourth brood, respectively, in 1927. For the summer individuals they mention 32 days as the maximum and 7 days as the minimum.

The results from the present investigation under various constant temperature combinations and relative humidities are given below:—

Effect of temperature on development.

(i) *Duration.*—Two sets of experiments were designed to ascertain the influence of temperature on the pupal stage (Table V). In one set, batches of pupae were kept at four different temperatures, in each case the temperature being the same as that at which the eggs and larvae were reared. The duration of the pupal period was found to decrease with rise of temperature, rapidly at the lower temperatures and very much less so at the higher. This applied to the three humidities at which the experiments were carried out. In the second set,

TABLE V.

Pupal period (days) under different conditions.

Temperature (°F.)		Relative humidity					
		100%		70%		35%	
Pupal stage at	Eggs and larvae reared at	No. of observations	Average period	No. of observations	Average period	No. of observations	Average period
65	65	32	19	56	20·8	18	24·5
75	75	132	14·3	50	15	78	17·3
85	85	134	12·0	94	13·0	90	14·2
95	95	12	11·0	25	11·5	7	12·5
85	75	104	11·2	94	12	No moth emerged out of 135 pupae	
85	65	44	16·4	24	22	One (out of 78 pupae)	15
65	85	76	21·5	38	23·2	30	25·2

some pupae derived from larvae reared at lower temperatures were transferred to a higher temperature and others from a higher to a lower temperature. From the results given in Table V it is concluded that rising temperatures in the spring shorten the duration of the pupal period and decreasing temperatures in the autumn lengthen it. The effect of this is to cause the adults to emerge early in the season and to lay eggs, the larvae from which are able to take advantage of new growth and consequently it is possible for more generations to be completed.

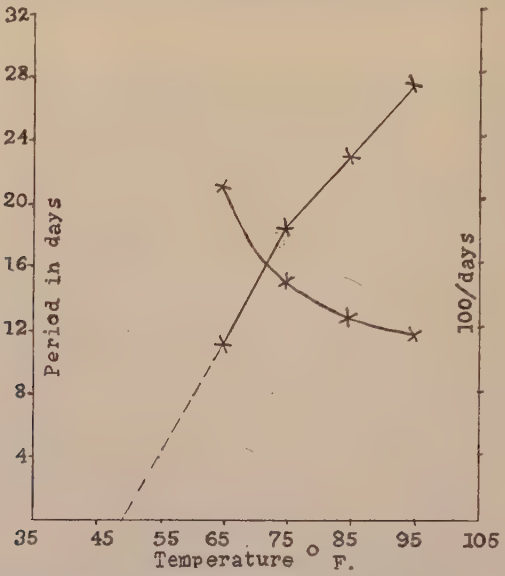


Fig. 5.—Pupal period of, and index of development for, pupae of *G. molesta* at constant temperatures and 100% relative humidity.

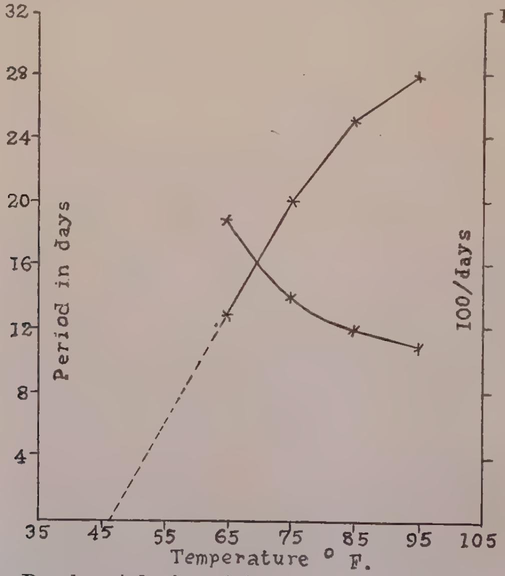


Fig. 6.—Pupal period of, and index of development for, pupae of *G. molesta* at constant temperatures and 70% relative humidity.

In the autumn there is a tendency for development to be arrested as winter conditions become more unfavourable.

(ii) *Threshold of development.*—An examination of figs. 5 to 7 shows that the theoretical threshold of development for the pupae lies at 46·5°, 49° and 52·5°F. at relative humidities of 100, 70 and 35 per cent., respectively. These figures seem to be very significant and indicate that under moist conditions the pupae are able to continue development at lower temperatures than those exposed to dry conditions. In areas with a moist climate, particularly those having relative humidities varying from 80 to 90 per cent., the pest could start development early in the spring and thus reach sufficiently large proportions to cause serious damage. On the other hand, under dry conditions the insect would continue to be inactive until the temperature had risen well above 52·5°F. and consequently would not build up its population so quickly.

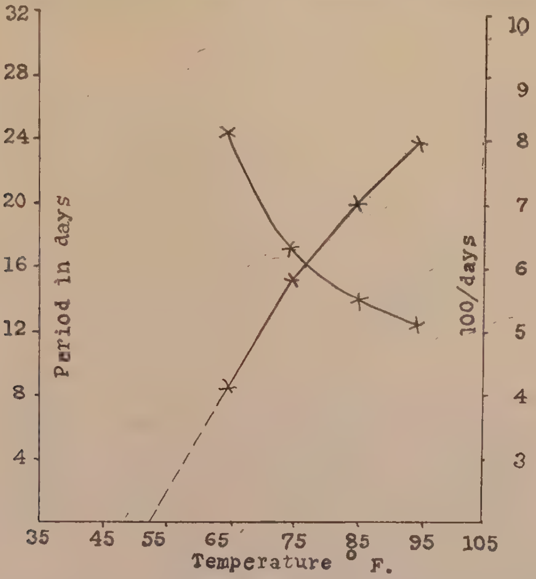


Fig. 7.—Pupal period of, and index of development for, pupae of *G. molesta* at constant temperatures and 35% relative humidity.

The threshold of development for the pupae is higher than that for the eggs or larvae and this helps the species to tide over inclement weather. Eggs and larvae which are not hibernating continue to develop even at low temperatures but, in the pupal condition, development would not proceed until warmer conditions prevailed and the eggs and subsequent larvae would be exposed to more favourable weather.

It is interesting to compare these data with those for *Carpocapsa pomonella* given by Shelford (1927). He calculated 50·1° and 51·4°F. as the threshold of development for relative humidities of 70 to 97 and 50 to 60 per cent., respectively. These figures are of much the same order as those for the Oriental Fruit Moth reported above, with the theoretical threshold of development lower at a high humidity than at a low humidity. The difference between the values at high and low humidities is greater in the case of the Oriental Fruit Moth, showing that this species has a greater preference for moist conditions for pupal development than *C. pomonella*.

(iii) *Optimum and upper vital limits.*—The indices of development (figs. 5 to 7) show that the rate of development slows down above 75°F. The decline is less steep at 100 per cent. R.H. than at 35 per cent. This decline is greater than that for the larvae, showing that higher temperatures are comparatively more detrimental to the pupae than to the larvae.

The effect of low temperatures on cocooning larvae was not determined as they are expected to tolerate the fairly low temperatures prevailing in temperate regions; this would not be materially different from other insects, particularly *C. pomonella* (Newcomer & Whitcomb, 1924).

Effect of humidity on development.

The published data here are extremely meagre. In fact, it is surprising that this important aspect should have received so little attention from workers in the past. As the pupal stage is generally passed outside the green tissues it may be considered likely that comparatively drier conditions would suit the pupae better. Present investigations show that this is not the case and that a saturated atmosphere was more favourable. It may be that, in nature, high humidity is maintained near the surface of the soil by evaporation of moisture from it and on account of the presence of luxuriant growth of grasses and weeds around the trees where most of the pupae are found. Frequent rains during the active season would also help in keeping the humidity high.

In these experiments the pupal period was found to be shortest at 100 and longest at 35 per cent. R.H. (Table V). A low relative humidity was extremely detrimental to pupae kept at 85°F. when they had been derived from eggs and larvae reared at 75° or 65°F., as very few moths emerged from a large number of pupae. The moths emerging at 100 per cent. R.H. and 95°F. were deformed and short lived, whilst those emerging at 70 per cent. R.H. were well formed, active and lived longer.

Effect of temperature and humidity on viability.

The viability of the pupae is influenced both by temperature and relative humidity. At the medium range of temperatures the affect of humidity is well marked. The data are presented in Table VI. A maximum viability of 71·8 per cent. was obtained at 75°F. and 100 per cent. R.H., whilst at 85°F. it was 68·36 per cent. The viability was always highest in a saturated atmosphere at all the combinations of temperature tried (except at 95°F.). Usually it was about one

TABLE VI.

Viability of pupae under different conditions.

Temperature (°F.)		Relative humidity								
Pre-pupae and pupae at	Eggs and larvae reared at	100%			70%			35%		
		No. of pupae	No. of moths emerged	Viability %	No. of pupae	No. of moths emerged	Viability %	No. of pupae	No. of moths emerged	Viability %
65	65	268	112	41·8	392	96	24·5	214	18	8·4
75	75	390	280	71·8	357	180	50·4	256	104	40·6
85	85	196	134	68·36	176	96	54·55	294	94	31·97
95	95	86	12	14·0	63	25	39·6	62	7	11·3
85	75	184	128	69·56	270	136	50·37	260	0	0·0
85	65	96	44	45·83	120	44	36·7	78	1	1·2
65	85	266	122	45·86	160	42	26·25	198	30	15·1

and a half times the figure for 70 per cent. relative humidity. The percentage viability was generally least at 35 per cent. R.H. and at one set of temperatures it was zero.

The viability of pupae exposed to 65°F. and 35 per cent. R.H. but resulting from larvae reared at 85°F. was almost double that of those which had been exposed throughout their entire life to 65°F. This means that a greater number of larvae which matured at higher temperatures were able to complete their development successfully at low temperatures combined with low humidity (to which the pupae were exposed) in comparison with those which were reared at low temperatures and the pupae exposed to both low temperature and humidity.

The viability at 35 per cent. R.H. is a little less than one third of that under saturated conditions at temperatures of 65°F. for pupae and 85°F. for the larval stage. This is rather significant, as, in areas of low humidity in late summer and early autumn, a lesser number of moths would emerge. Consequently, the damage to fruit in those areas is likely to be less. On the other hand, places which are more humid at that time may have a larger emergence of moths with a greater likelihood of damage to fruits from the late broods of larvae.

Larval Diapause.

The larvae enter diapause in late summer and autumn to tide over unfavourable weather and food conditions. The larvae spin thick silken cocoons in which they rest for an extended period before transforming into pupae. Several workers have attempted to investigate the causes which initiate diapause. These may be falling temperatures in the autumn, some change in the quality and water content of food, relative humidity, photoperiodism, hormones or some inherent factors. These have been very ably reviewed by Dickson (1950). Although the present investigation was not directed towards finding out the factors responsible for inducing diapause, several interesting features have been revealed.

The period of diapause may be classed as "short" if it is 31–60 days, and "long" if it exceeds this. Larvae belonging to both of these categories were found among those reared at various constant temperatures and relative humidities.

Short diapause.

Larvae entering short diapause were found at constant temperatures of 65°, 75° and 85°F. and at some of the variable temperatures (Table VII). The greatest number of larvae in this category was found among those reared at 75°F. and then transferred to 85°F. during the cocoon period, followed by that at a constant temperature of 75°F. throughout, and after that by the number reared at 65°F. and later kept at 85°F. during the cocoon period. Larvae reared at 75° and 85°F. and then transferred to 65°F. did not enter into short diapause, but for the most part went into long diapause. This period of short diapause appears to be different from the period of quiescence which is induced by low temperatures and easily terminated when the material is transferred to a high temperature, as it came even at optimum temperatures. In fact, the largest number and longest period of short diapause was in the case of larvae reared at the optimum temperature of 75°F. Some even entered diapause at the relatively high temperature of 85°F. It could not have been the result of unfavourable temperature or humidity, or even food, as the same kind of food was given in all cases. It would not be due to the effect of light as all the material was reared in darkness except for the time of taking daily observations. This phenomenon appears to be based more on genetic factors than anything else.

The effect of humidity is rather distinct (Table VII). At a constant temperature of 65°F., a few larvae entered short diapause at 100 per cent. R.H., but none did so at 70 and 35 per cent. R.H. At 75°F. a large number entered diapause, the number and period decreasing with the rise of humidity. At 100 per cent. R.H. none entered short diapause at 85°F. but a few did so in drier conditions. A fairly large number of cocooning larvae kept at 85°F., with feeding period at 75°F., entered short diapause under more moist conditions, but there were fewer at 100 per cent. R.H. than at 70 per cent., whilst at 35 per cent. not a single moth emerged from 135 cocoons. Several cocooned larvae at 85°F. with rearing period at 65°F. entered diapause at 70 per cent. R.H. but none entered diapause at 100 per cent. R.H. and over 98 per cent. died without emerging as moths at 35 per cent. R.H. The duration of short diapause at 85°F. was almost the same whether the larvae had been reared at 75° or 65°F. but those reared at 65°F. produced no diapausing larvae at 100 per cent. R.H., all emerging as moths within a reasonable period. Mortality of cocooned larvae was almost complete at 35 per cent. relative humidity, under similar temperature conditions.

TABLE VII.

Period of short diapause plus period of pupation for medium-cycle larvae * under different conditions.

Temperature (°F.)		Relative humidity					
		100%		70%		35%	
Period at	Eggs and larvae reared at	Average period (days)	No. of observations	Average period (days)	No. of observations	Average period (days)	No. of observations
65	65	39	8	Nil	Nil	Nil	Nil
75	75	46·7	8	49	15	53	18
85	85	Nil	Nil	35	2	44·5	4
85	75	34·3	24	34·8	42	Nil	Nil
85	65	Nil	Nil	34·4	20	Nil	Nil
65	85	Nil	Nil	Nil	Nil	Nil	Nil
65	75	Nil	Nil	Nil	Nil	Nil	Nil

* Total period extending from 31 to 60 days (see p. 887).

These results suggest that the species may overcome unfavourable conditions, brought about by low humidity, by entering short diapause in the prepupal stage though the prevailing temperature may be optimum; survival results unless the humidity is so low that it is fatal when prevailing over an extended period.

Long diapause.

The data on long diapause (true diapause) under various conditions studied in the course of the present work are given in Tables VIII and IX. An examination of these Tables shows that the larvae went into diapause at constant temperatures of 65° and 75°F. and under variable temperatures when cocoons formed by larvae reared at 75° and 85°F. were transferred to 65°F. The feeding larvae as well as the cocooned larvae and pupae were kept in total darkness except for short periods when they were taken out for examination or the doors of the incubators and refrigerators were opened for other observations.

None of the larvae entered diapause when kept at 85°F., whether they were reared at 85°, 75° or 65°F. This simulates spring and mid-summer conditions. The period of two months' diapause at 79°F. mentioned by Dickson (1950) appears

TABLE VIII.

Period of diapause plus period of pupation for long-cycle larvae * under different conditions.

Temperature (°F.)		Relative humidity											
		100%				70%				35%			
		Period in days			No. of observations	Period in days			No. of observations	Period in days			No. of observations
Diapausing larvae and pupae kept at	Eggs and larvae reared at	Average	Maximum	Minimum		Average	Maximum	Minimum		Average	Maximum	Minimum	
65	65	139	241	75	72	110	137	88	8	No moth emerged from diapausing larvae			
						140	170	109	32†				
75	75	87·7	126	62	140	76·6	104	63	15	74	85	67	8
85	85	<—				None entering diapause				—>			
85	75	<—				None entering diapause				—>			
85	65	<—				None entering diapause				—>			
65	85	132·5	184	124	46	109·5	143	76	4	No moth emerged from larvae entering diapause			
65	75	162	179	113	18	130	160	110	17	No moth emerged from larvae entering diapause			

* Total period more than sixty days.

† Diapausing larvae transferred to room temperature and 100% relative humidity on 10th March 1951.

to belong to the category of short diapause. The relative influence of temperatures prevailing during the feeding period and the cocoon period is quite clear.

Dickson (1950) studied some of the factors governing the induction of diapause in the Oriental Fruit Moth. He postulated that diapause in the larvae of this moth is induced by a hormone or hormone-like substance that is produced by the larva during the larval feeding period. He further concluded that this hormone is produced by a two-phase reaction, which required darkness for one phase and light for the other and that the induction of diapause is controlled by temperature and daily exposure to light during the larval feeding period. According to him very few larvae grown in the absence of light entered diapause. The present observations do not support his theory, particularly with regard to the effect of light. As will be seen from Table IX, 64·3 per cent. larvae successfully completed diapause and emerged as moths, even though they were reared in total darkness at 65°F., and 50 per cent. when reared throughout at 75°F. Larvae reared at 75° and 85° and kept at 65°F. also went into diapause in fairly large numbers, particularly at 100 per cent. R.H. The actual number of larvae which went into diapause must be much higher than the number of moths emerging from them as there would naturally be considerable mortality in the hibernating stock.

TABLE IX.

Percent. emergence of moths under different conditions.

Temperature (°F.)		Percentage of moths emerging from larvae in								
Diapausing larvae and/or pupae kept at	Eggs and larvae reared at	Short cycle*			Medium cycle*			Long cycle*		
		Relative humidity %			Relative humidity %			Relative humidity %		
		100	70	35	100	70	35	100	70	35
65	65	28·57	58·33	100	7·13	0·0	0·0	64·3	41·67	0·0
75	75	47·14	60·0	75·0	2·86	20·0	17·3	50·0	20·0	7·7
85	85	100	97·9	95·74	0·0	2·1	4·26	0·0	0·0	0·0
85	75	81·25	69·1	0·0	18·75	30·9	0·0	0·0	0·0	0·0
85	65	100	54·5	100	0·0	45·5	0·0	0·0	0·0	0·0
65	85	62·3	90·5	100	0·0	0·0	0·0	37·7	9·5	0·0
65	75	47·0	75·0	100	0·0	0·0	0·0	53·0	25·0	0·0

N.B.—The total number of moths that emerged under different conditions is shown in Table VI. The figures under short, medium and long cycle at different humidities in this Table are derived from Tables V, VII and VIII, respectively, and are given here as a percentage of those in Table VI. (* For definitions see p. 887.)

The initiation of diapause in the Oriental Fruit Moth larvae appears to be due to an inherent characteristic and may to some extent be governed by the nature and quality of food on which the larvae are fed. Dickson (1950) used small immature apples to feed the larvae, whereas, in the present investigation, they were fed on almost mature apples picked in August and stored at about 50°F. until needed. This difference in food in the two investigations may to some extent be responsible for some of the conflicting results obtained. Larvae reared during April, May and June 1951 on the same kind of apples stored at about 50°F. did not, with very few exceptions, enter diapause. Isely (1939) could not find any relationship between the transformation of the larvae of *Carpocapsa pomonella* and the relative ripeness of the fruit on which they were fed.

The relative humidity to which the hibernating larvae are exposed seems to have a great influence on the extent and successful completion of diapause. The actual number of larvae going into diapause was not determined in these experiments as they were not disturbed in the cocoons, but the proportion is believed to be fairly high. Squire (1940) reported that the diapause in the larvae of Pink Bollworm, *Platyedra gossypiella* (Saund.) depends upon the moisture content of the seeds in which they feed. In the case of the Oriental Fruit Moth the question of the water content of the food is relatively unimportant. An examination of Tables VIII and IX shows that relative humidity acts more on the prepupal and pupal stages. None of the larvae in diapause kept at 35 per cent. R.H. at any temperature, with the exception of those at 75°F., emerged as moths. At 75°F. there was only 7·7 per cent. emergence. The emergence from diapause was most successful at 100 per cent. R.H. and to an appreciable extent at 70 per cent. R.H.

Emergence under different Conditions.

The percentage of moths emerging from larvae of different cycles under various conditions is shown in Table IX. The larvae, according to the present investigation, can be divided into the following categories:—

Short-cycle larvae.—Those larvae in which the prepupal plus pupal period was much less than 30 days under any set of conditions. They pupated soon after spinning cocoons and emerged as moths.

Medium-cycle larvae.—Those larvae in which the prepupal plus pupal period varied from 31 to 60 days (short diapause). At the end of this period they emerged as moths.

Long-cycle larvae.—Those which entered into a long diapause of over 60 days irrespective of temperature and humidity. At the end of this period they emerged as moths without being transferred to another set of conditions.

It may be noted, however, that these larvae represent only those which were able to complete their life-cycle successfully and finally emerge as moths. The actual number belonging to each category must have been larger, particularly in the long-cycle class, many of which might have died in the cocoons.

The larval duration in respect of the three categories has been given in Tables V, VII and VIII. The relative proportions of those which completed their life-cycles as based on the emergence of moths under different conditions are given in Table IX, from which it will be seen that at a constant temperature of 65° and 75°F. larvae of all categories were found. At a constant temperature of 85°F., larvae were mostly in the short cycle, some in medium but none in the long cycle, whether the larvae were fed at 85°, 75° or 65°F. before they were exposed to 85°F. If the larvae reared at either 75° or 85°F. were kept at 65°F. during their cocoon period they fell into the category of short-cycle or of long-cycle larvae; none emerged as moths under the medium cycle.

The effect of relative humidity is well marked. The data in Table IX indicate that, in areas where low relative humidity prevails during late summer and early autumn, the larvae of the Oriental Fruit Moth have a strong tendency to pupate and emerge as adults and not go into hibernation. Under such conditions the pest would remain active for a longer period and consequently suffer from subsequent severe cold spells. Hibernation of the cocooned larvae is absolutely essential for the survival of the pest in temperate regions but, if the conditions are dry, very few larvae would enter diapause or complete it successfully and very few moths would emerge in the following spring on the return of favourable conditions. On the other hand, substantially larger numbers of larvae enter diapause or complete it successfully if the relative humidity to which they are exposed is high enough. This ensures greater survival of the species in regions where high humidity prevails in later summer and autumn. Thus the present geographic distribution of the pest appears to be largely governed by the relative humidity prevailing from July to November, the period when larvae enter diapause.

In the case of *Carpocapsa pomonella*, hot and dry conditions are considered more favourable. Cutright (1937) has reported from Ohio that, in hot and dry seasons, injury to apple by the larvae of *C. pomonella* appeared early and increased rapidly while in a cool wet season it was the reverse. Therefore, the two species although resembling each other in several respects may not necessarily be equally serious in the same region. If one is more abundant than usual in an area or in a particular season it is most likely that the other one may not be so, and *vice versa*.

Fecundity under different Conditions.

Effect of Temperature and Humidity on Fecundity.

The fecundity of *G. molesta* under insectary and near-orchard conditions has been extensively studied in the past. Stearns & Peterson (1928) got an average of 7, 23 and 40 eggs per female for the first, second and third brood moths in New Jersey.

Dustan & Armstrong (1933) carried out some experiments on the influence of temperature and moisture on the adults of the Oriental Fruit Moth in Toronto, Canada. They found that the females laid 98 per cent. of the daily total of eggs during the late afternoon, from three hours before to one hour after sunset. The hour of maximum deposition was that starting two hours before sunset. In their experiments the moths stopped egg-laying completely when in total darkness. Under more or less controlled temperature conditions the data for selected moths given by Dustan & Armstrong (1933) were 4, 135 and 114 eggs per female at a temperature range of 94·5 to 96·3°F., 88·8 to 90·8°F. and 79·3 to 85·4°F., respectively, but the number of moths liberated in each battery jar was not mentioned. This only shows that some moths did lay eggs at high temperatures. The pre-imaginal life-history of the moths was not given. In another set of experiments, they obtained an average of 29·3 eggs per female, when the females were supplied with moisture and liberated in cages having moist sand at the bottom, as compared with 7·15 eggs per female in the case of moths kept in dry cages and not supplied with moisture. High humidity at the time of oviposition is thus more conducive to egg-laying than low humidity. If this is true, the moths may not be able to lay their full quota of eggs on plants in areas in which the relative humidity is low, particularly in the afternoon and evening.

In the present investigation, moths emerging from pupae kept under different conditions were liberated in small cages described earlier (page 871). In order to provide suitable material for oviposition an almost continuous supply of peach seedlings was maintained in the greenhouse. In the case of this species it was found extremely difficult to obtain eggs from individual pairs liberated in the cages, consequently, several pairs were kept together at various temperatures. On several occasions only a small number of males and females would emerge from the same stock on any one day and, in these cases, moths emerging over a period of several days were kept together in the same cage. As a result of this it was not possible to determine the preoviposition, oviposition and postoviposition periods for the moths or the longevity of the two sexes. However, a record of the number of males and females added or dying each day was maintained. The moths were fed on thin sugar solution absorbed in cotton wads.

The observations are given in Table X. The pre-imaginal as well as the imaginal life was always in darkness.

Effect of temperature.

It will be seen (Table X) that generally the females laid very few eggs and many died without laying any. Whether this was due to darkness cannot be said definitely as the provision of light in some cases did not improve the amount of oviposition. The optimum temperature for egg-laying was 75°F. constant. Moths kept at 65°F. from cocoons at 65°F., and from larvae reared at 75° or 85°F. laid very few eggs, the highest average being 4·3. These conditions are somewhat similar to those in the case of moths from overwintering material. The spring-brood moths are known to lay very few eggs.

TABLE X.

Fecundity under different conditions.

Temperature (°F.)			Relative humidity at which pupae were kept					
Adults at	Pupae kept at	Eggs and larvae reared at	100%		70%		35%	
			Average no. of eggs per female	No. of pairs	Average no. of eggs per female	No. of pairs	Average no. of eggs per female	No. of pairs
65	65	65	0·3	26	0·5	24	0·0	8
75	75	75	12·7	48	8·7	20	6	26
85	85	85	6·2	40	9·8	38	2·2	27
85	85	65	0·3	20	0·0	20	Very few moths	
65	65	85	0·0	28	4·3	16	0	14
85	85	75	11·3	42	3·4	28	No moths emerged	
65	65	75	0·25	12	1·0	24	0·0	7
75	65	65	7·46	13	—	—	—	—

Effect of humidity.

The effect of low humidity during the cocoon life on the fecundity of moths is pronounced (Table X). Generally, maximum oviposition was from material exposed to 100 per cent. R.H. and very few eggs were laid by moths whose pupae had been kept at 35 per cent. R.H. It is therefore, evident that low humidity during the cocoon period is injurious to fecundity. Low relative humidity, therefore, is not only injurious to the development of the species but is also equally or even more harmful to the egg-laying capacity of the moths.

Experiments at room temperature.

In addition to experiments at constant temperatures and humidities, moths emerging from material reared at an ordinary room temperature of 70 to 80°F. were liberated in large cages, 10″ × 10″ × 8″, kept over moist sand in enamel trays. The eggs laid by these moths were counted every day. The oviposition of these moths is recorded in Table XI.

The highest average of 74·5 eggs per female, based on observations of 105 pairs reared on apples, was obtained during the period 24th September to 15th October 1950. In February 1951 the average was lowest, *i.e.*, 3·3 eggs per female. This may be due to the fact that the moths had emerged from overwintering cocoons.

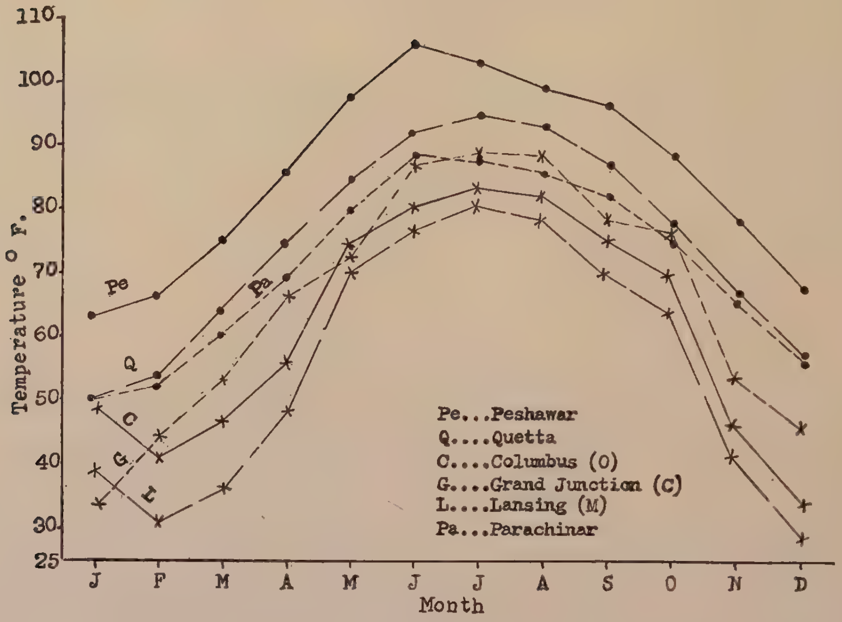


Fig. 8.—Mean maximum temperature (°F.) 1950.

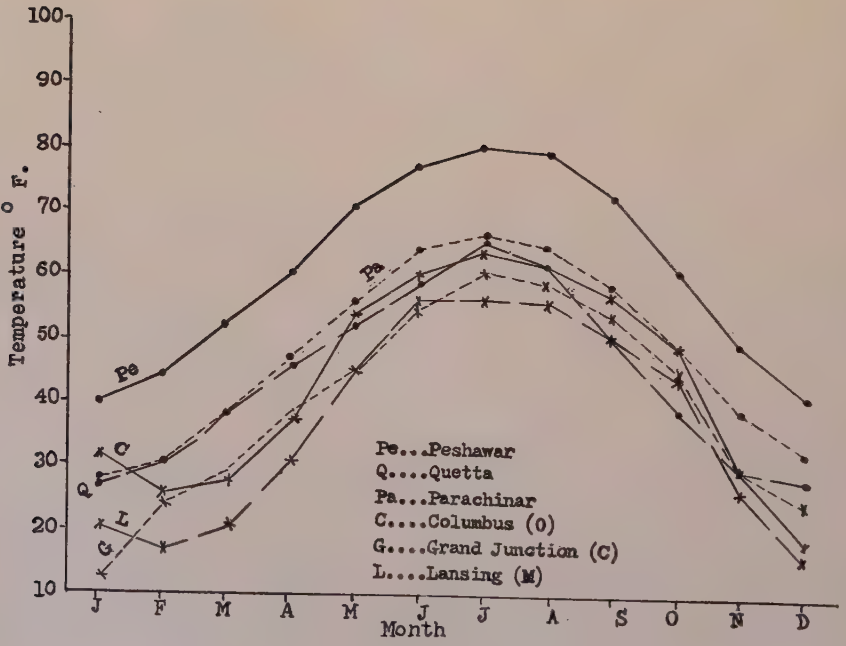


Fig. 9.—Mean minimum temperature (°F.) 1950.

The greater oviposition under these conditions as compared with that under controlled conditions previously described may have been due to the effect of wide fluctuation in temperature, the larger size of the cages, the greater number of moths in each cage, the presence of light in the room during the day and the relative length of day and night in different months.

TABLE XI.

The fecundity of *G. molesta* at room temperature (70–80°F.).

Period	No. of pairs	Total no. of eggs	Average no. of eggs per female	Source of material
1950				
May	12	5	0·4	Overwintering larvae
July	30	1260	42·0	Larvae from peach shoots
1–15 Aug.	24	1166	48·6	Larvae from peach shoots
16–31 Aug.	35	1630	46·6	Larvae reared on Jonathan apples stored at about 50°F.
1–7 Sept.	14	462	33	„
8–15 Sept.	54	1885	35	„
16–30 Sept.	50	2210	44	„
24 Sept.–15 Oct.	105	7827	74·5	„
16–31 Oct.	50	1847	37·0	„
Nov.	16	150	9·4	„
1951				
Jan.	17	156	9·2	„
Feb.	21	70	3·3	„
Mar.	44	424	9·6	„
Apr.	34	316	9·3	„
May	40	2284	57·1	„
1–15 June	36	2355	65·4	„

There was wide fluctuation in the average for different periods during the year, even in the laboratory where conditions were almost similar throughout, and it is impossible to postulate the real cause or causes without further investigation. It may be that successive generations lay varying numbers of eggs which may be controlled by (among other things) genetical factors.

METEOROLOGICAL DATA AND INCIDENCE.

Meteorological data for the years 1948–50 for three inland peach-growing localities in the United States and three in Pakistan have been studied. These data were plotted, but as the relative trend of the curves is very similar for the three years, only the graphs for 1950 are shown here (figs. 8–13). The localities in question are, in the United States, Columbus, Ohio (latitude, 39°58′N.; longitude, 83°W.; elevation, 724 ft.); Grand Junction, Colorado (latitude, 39°06′N.; longitude, 108°32′W.; elevation, 4,849 ft.) and Lansing, Michigan (latitude, 42°47′N.; longitude, 84°36′W.; elevation, 859 ft.), whilst those

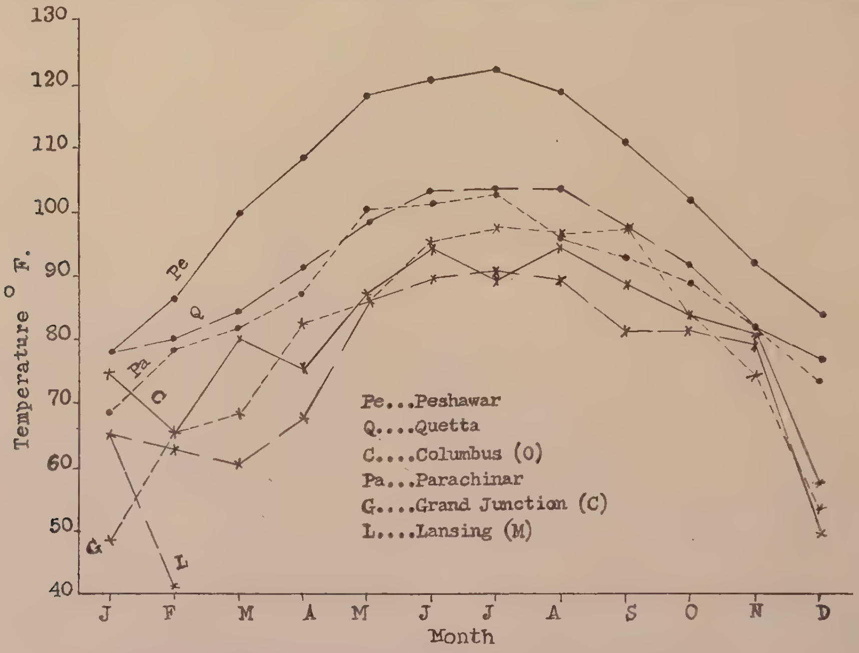


Fig. 10.—Highest temperature (°F.) during each month, 1950.

in Pakistan are Parachinar (latitude, 33°55′N.; longitude, 70°5′E.; elevation, 5,784 ft.), Quetta (latitude, 30°10′N.; longitude, 67°E.; elevation, 5,508 ft.) and Peshawar (latitude, 34°N.; longitude, 71°37′E.; elevation, 1,149 ft.).

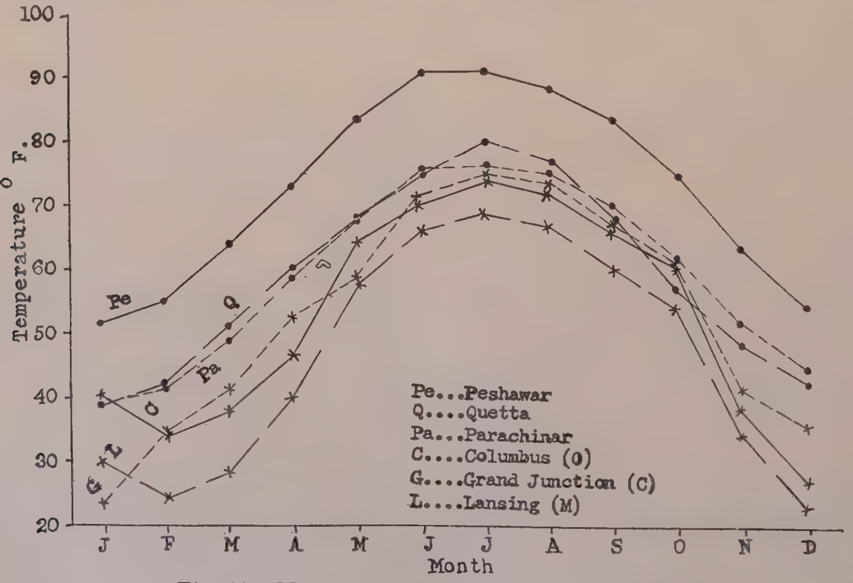


Fig. 11.—Mean monthly temperature (°F.) 1950.

It will be seen (fig. 8) that the mean maximum temperatures in June to September are higher in Pakistan than in the United States at the stations mentioned, with the possible exception of Parachinar. For the remaining months temperatures are on the whole much higher in Pakistan than those in the United States for the stations under discussion. The highest temperature recorded at the American stations in 1950 ranged between 90° and 94°F., whilst in Pakistan 102°F. was registered at Parachinar, 103°F. at Quetta and 122°F. at Peshawar (fig. 10). During 1948, the highest temperatures at Parachinar and Quetta were below 98°F., almost the same as those at Columbus, Grand Junction and Lansing. Although the temperatures for Pakistan stations were generally a few degrees higher than those for the American stations, they were within the upper vital limits for the various stages of the Oriental Fruit Moth at Parachinar and Quetta;

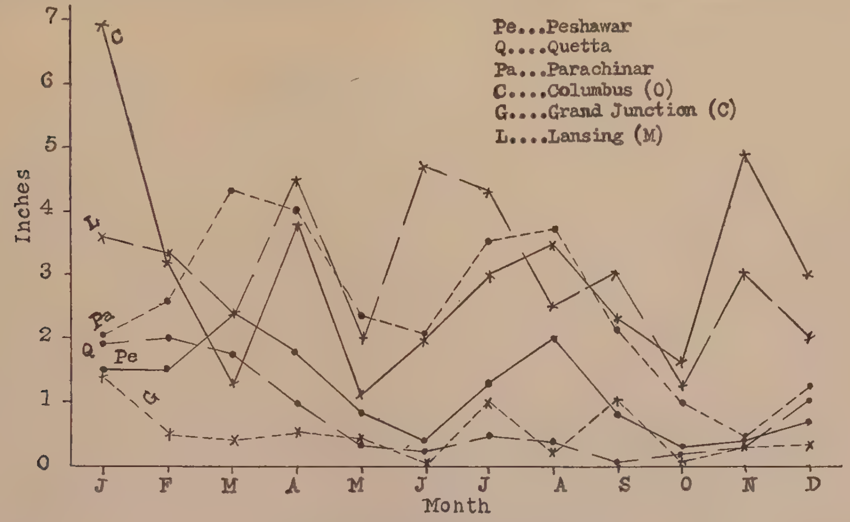


Fig. 12.—Monthly rainfall, 1950.

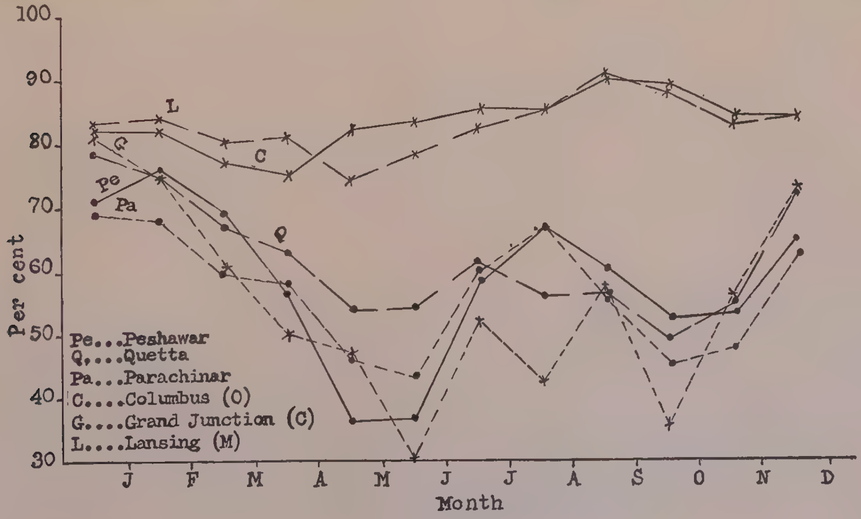


Fig. 13.—Mean relative humidity, 1950.

the averages of daily minima and mean monthly temperatures at the two latter stations were, in the main, a few degrees above those for the stations in the United States. These temperatures were near the optimum for the pest, especially during the summer and autumn, and would not affect its development adversely. At Peshawar, however, the temperatures were often much beyond the upper vital limits of the insect.

Rainfall at Columbus, Lansing and Parachinar from May to September was much more than that at Grand Junction and Quetta (fig. 12).

The data with regard to relative humidity are rather interesting (fig. 13). At Columbus and Lansing it was rarely below 80 per cent., usually between 80 and 90 per cent. throughout the year, and far in excess of that at Grand Junction and the Pakistan stations. The intensity of attack of the moth is highest at Columbus and least at Grand Junction and, although the pest is present at the latter place, it has seldom attained the status of a major pest. This corroborates the findings in the laboratory, based on constant temperature and humidity experiments, that low humidity, particularly in the late summer and early autumn, is highly detrimental to the development of the pest, and probably limits its geographic distribution.

In spite of good rainfall at Parachinar from May to September the relative humidity remained relatively low. Parachinar is situated on a slope of the mountains and it appears that quick drainage of rainwater to lower levels prevents the rise of relative humidity. There were 5 to 7 rainy days every month and big downpours on a few days.

The relative humidity at Quetta is similar to that at Grand Junction between May and September but temperatures run higher. At Peshawar the relative humidity was also relatively low but the temperatures were mostly high, often going beyond the upper vital limits for the Oriental Fruit Moth.

There is, therefore, little likelihood of the pest becoming established at Peshawar. *Carpocapsa pomonella*, with which *G. molesta* is often compared, is not known to exist at Peshawar. There is a likelihood of the Oriental Fruit Moth becoming established if it were introduced into the Quetta area, particularly at Ziarat (elevation over 8,000 ft.), where the rainfall in summer is higher. There is also a distinct possibility of the insect becoming at least a minor pest in the Parachinar area if by any chance it gained access to the region. *C. pomonella* is already doing serious damage in Quetta and Parachinar, where it is believed to have been introduced not long ago. Although there are some areas where in all probability the Oriental Fruit Moth would not become a pest, *e.g.*, Peshawar, there are several other regions in Pakistan and India, with meteorological conditions similar to those in the United States, where the insect could become a pest if unfortunately it were introduced. It is, therefore, necessary on the part of the plant quarantine organisations of those countries to continue to adopt strict quarantine measures in order to prevent the introduction of the Oriental Fruit Moth.

Summary and Conclusions.

A study of the development and fecundity of the Oriental Fruit Moth, *Grapholitha molesta* (Busck), under controlled temperatures of 60°, 65°, 75°, 85° and 95°F. and relative humidities of 35, 70 and 100 per cent. was carried out at East Lansing, Michigan, in 1950–51. The technique adopted is described.

The incubation period of the eggs decreased from 7–8 days at 60°F. to 2·76 days at 94°F., increasing to 3·56 days at 95°F. A large number of eggs withstood an exposure of 40 hours at 98°F., but an exposure of 48 hours proved fatal. An exposure of 21 hours to 105°F. reduced the viability of eggs to 25–43 per cent. and increased the incubation period by 36–40 hours.

The influence of relative humidity on the development of eggs, though significant, was not well marked. The influence of relative humidity seemed to be more marked on the viability than on the incubation period, conditions near saturation point being much more favourable than dry conditions.

It is evident from the data that the eggs of the Oriental Fruit Moth can tolerate fairly high temperatures and low humidities. It is thought that the flattened and scale-like form of the eggs may help them to resist the effect of adverse conditions.

The average feeding period of the larvae varied from 36·81 days at 65°F. to 18·0 days at 95°F. There were large individual variations within any given batch of larvae kept under uniform conditions.

The duration of the pupal stage (short cycle) decreased with the rise of temperature from 19 days at 65°F. to 11 days at 95°F., decreasing rapidly at first and very much less so at the higher temperatures. The temperature at which the larvae were reared had a distinct influence on the duration of the pupal period at other temperatures. Pupae kept at 65°F., developing from larvae reared at 85°F., had a longer pupal duration than those at other combinations of temperatures. The pupal period was found to be shortest at 100 and longest at 35 per cent. relative humidity. The viability of pupae was always highest in a saturated atmosphere at all the combinations of temperature tried. Consequently, low humidity in late summer and early autumn will affect adversely the number of moths to emerge, and the damage to fruits in areas where such conditions exist is likely to be negligible. On the other hand, more humid conditions at this time of year will favour the emergence of moths, and proportionately greater damage to fruits from the late broods of larvae will result.

The theoretical threshold of development for eggs is found to be between 40° and 44°F. depending upon the relative humidity, lowest at 100 per cent. and highest at 35 per cent. relative humidity. For larvae it is 43·5°F.; whereas for pupae it varies from 46·5° to 52·5°F. at relative humidities of 100 and 35 per cent., respectively. In moist conditions, unlike dry conditions, the eggs and the pupae (the two stages affected by humidity) will continue to develop at lower temperatures. In areas with a moist climate, particularly those having relative humidities varying from 80 to 90 per cent., the insect can start development early in the spring and thus increase to large proportions causing serious damage. The differences between the thresholds of development for the various stages at high and low humidities are greater for the Oriental Fruit Moth than for the Codling Moth, *Carpocapsa pomonella* (L.), showing that the former prefers more moist conditions for its development.

The larvae of the Oriental Fruit Moth were found to enter either a short diapause (medium cycle) for a period of 31 to 60 days, or a long diapause (long cycle) with a duration of over 60 days under various temperatures and humidities. The largest number and longest period of short diapause was in the case of larvae reared at the optimum temperature of 75°F. and kept as cocoons at 75° or 85°F. When reared at 75°F. throughout, more larvae entered short diapause under dry than humid conditions.

The maximum duration of long diapause, including the pupal period, at 100 per cent. R.H. was: 241 days at 65°F. (larvae reared at 65°F.); 184 days at 65°F. (larvae reared at 85°F.); 179 days at 65°F. (larvae reared at 75°F.) and 126 days at 75°F. (larvae reared at 75°F.). The emergence from diapause was most successful at 100 per cent. relative humidity and to an appreciable extent at 70 per cent. R.H. Photoperiodism did not have any appreciable effect on the induction of diapause, as 64·3 and 50 per cent. larvae successfully completed diapause and emerged as moths, even though they were reared in total darkness at 65° and 75°F., respectively. Diapause in the larvae of the Oriental Fruit Moth appears to be an inherent characteristic and to some extent may be influenced by the nature and quality of the food on which they are reared.

The percentage of moths emerging under different conditions is given. At 35 per cent. R.H. very few larvae entered long diapause and practically all the moths emerged after a cocoon period of less than a month. Generally about half of the total moths emerged from long-cycle larvae if the relative humidity had been 100 per cent. during the cocoon period; about one third if it had been 70 per cent.; and nil at 35 per cent. R.H., except 7·7 per cent. at 75°F. This indicates that the larvae of the Oriental Fruit Moth, in areas where low relative humidity prevails during late summer and early autumn, largely emerge as moths and do not go into hibernation. If the conditions are dry, very few larvae enter diapause or complete it successfully and few moths will emerge in the following spring on the return of favourable conditions. On the other hand, a substantially larger number of larvae may enter diapause and complete it successfully if the relative humidity to which they are exposed during the cocoon period is high enough. The latter adaptation favours greater survival of the species in regions where high humidity prevails in late summer and autumn. The present geographical distribution of the Oriental Fruit Moth, therefore, appears to be largely governed by the relative humidity prevailing from July to November, the period when the larvae enter diapause. In humid areas, *G. molesta* is far more abundant than in the drier regions, a difference that is explained here by the influence of relative humidity on its development and on the successful completion of larval diapause.

Under controlled conditions, the optimum range of temperature for egg-laying was 75° to 85°F. The moths laid eggs when kept in darkness but the total number of eggs was few, the highest average per female being 12·7. In breeding experiments under uncontrolled laboratory conditions, the females emerging from the overwintering cocoons laid very few eggs compared to those from the short-cycle larvae. The fecundity of moths emerging from cocoons kept at low humidities was generally lower than that of those with pre-imaginal life under high humidities. The difference, however, is not well marked between 100 and 70 per cent. relative humidity. Moths emerging from material reared at an ordinary room temperature of 70–80°F. laid on an average 74·5 eggs per female during the period 24th September to 15th October 1950. In the months of November 1950 to April 1951, the average per female varied from 3·3 to 9·6 eggs in the laboratory. The average increased to 57·1 eggs during May 1951 and to 65·4 during June. There was wide fluctuation in the average number of eggs laid per female at different times of the year in the laboratory, where temperature conditions were almost the same throughout the year. Moths of successive generations, even though fed on the same food in their larval stage, laid a varying number of eggs.

Meteorological data for 1950 for three typical stations in the United States of America have been compared with those of three places in Pakistan. The probability of this insect becoming at least a minor pest in places like Parachinar and Ziarat (Pakistan), where the maximum temperature seldom rises above 98°F. and the relative humidity is often around 50–60 per cent., is rather high. It is, therefore, necessary on the part of the plant quarantine organisations of Pakistan and India to continue to adopt strict measures in order to prevent the introduction of the Oriental Fruit Moth into those countries.

Acknowledgements.

The writer wishes to express his sincere appreciation and thanks to Professor Ray Hutson, Head of the Department of Entomology, Michigan Agricultural Experiment Station, for guidance, criticism, help and constant encouragement in the conduct of this work.

The author is indebted to Dr. W. B. Drew, Dr. C. J. Alexopoulos, Dr. E. S. Beneke, Professor D. Cation and Dr. H. L. King for their generous help in certain aspects of this investigation.

References.

Alden, C. H. & Clarke, W. H. (1931). The life history and control of the Oriental Fruit Moth.—Bull. Ga Bd Ent., no. 74, 23 pp.

Allee, W. C., Emerson, A. E., Park, O., Park, T. & Schmidt, K. P. (1949). Principles of animal ecology.—837 pp. Philadelphia, Saunders.

Cutright, C. R. (1937). Codling Moth biology and control investigations.—Bull. Ohio agric. Exp. Sta., no. 583, 45 pp.

441 Dickson, R. C. (1950). Factors governing the induction of diapause in the Oriental Fruit Moth.—Ann. ent. Soc. Amer., **42,** pp. 511–537.

Dustan, G. G. & Armstrong, T. (1933). Observations on the relation of temperature and moisture to the Oriental Peach Moth.—63rd Rep. ent. Soc. Ont., 1932, pp. 29–39.

Eddy, C. O. & Nettles, W. C. (1931). Biological studies of the Oriental Fruit Moth, 1930.—Bull. S. C. agric. Exp. Sta., no. 278, 21 pp.

Froggatt, W. W. (1914). The Peach Tip Moth.—Agric. Gaz. N.S.W., **25,** pp. 413–414.

Garman, P. (1917). The oriental peach pest (*Laspeyresia molesta* Busck), a dangerous new fruit insect of Maryland.—Bull. Md agric. Exp. Sta., no. 209, 16 pp.

Garman, P. (1930). The Oriental Peach Moth in Connecticut.—Bull. Conn. agric. Exp. Sta., no. 313, pp. 401–451.

Glenn, P. A. (1922). Codling-moth investigations of the State Entomologist's Office, 1915, 1916, 1917.—Bull. Ill. nat. Hist. Surv., **14,** pp. 219–289.

Haeussler, G. J. (1940). General information concerning the Oriental Fruit Moth in Japan and Chosen.—J. econ. Ent., **33,** pp. 189–193.

Harukawa, C. (1923). Second notes on the Oriental Peach Moth, *Laspeyresia molesta* Busck.—Ber. Ōhara Inst., **2,** pp. 235–258.

Harukawa, C. (1929). Relation of temperature to the growth of Oriental Peach Moth. I.—Ber. Ōhara Inst., **4,** pp. 67–94.

Heinrich, C. (1926). Revision of the North American moths of the subfamilies Laspeyresiinae and Olethreutinae.—Bull. U.S. nat. Mus., no. 132, p. 28.

Hodgman, C. D. *Ed.* (1949). Handbook of chemistry and physics, p. 1951.—Cleveland, Ohio, Chem. Rubber Publ. Co.

Isely, D. (1939). Timing seasonal occurrence and abundance of the Codling Moth.—Bull. Ark. agric. Exp. Sta., no. 382, 26 pp.

Krogh, A. (1914). On the influence of temperature on the rate of embryonic development.—Z. allg. Physiol., **16,** pp. 163–177.

Newcomer, E. J. & Whitcomb, W. D. (1924). Life history of the Codling Moth in the Yakima Valley of Washington.—Bull. U.S. Dep. Agric., no. 1235, 76 pp.

Peterson, A. & Haeussler, G. J. (1930). Life history of the Oriental Peach Moth at Riverton, N.J., in relation to temperature.—Tech. Bull. U.S. Dep. Agric., no. 183, 37 pp.

QUAINTANCE, A. L. & WOOD, W. B. (1916). *Laspeyresia molesta*, an important new insect enemy of the peach.—J. agric. Res., **7**, pp. 373–377.

SANDERSON, E. D. & PEAIRS, L. M. (1913). The relation of temperature to insect life.—Tech. Bull. N.H. agric. Exp. Sta., no. 7, 125 pp.

SHELFORD, V. E. (1927). An experimental investigation of the relations of the Codling Moth to weather and climate.—Bull. Ill. nat. Hist. Surv., **16**, pp. 311–440.

SNAPP, O. I. & SWINGLE, H. S. (1929). Life history of the Oriental Peach Moth in Georgia.—Tech. Bull. U.S. Dep. Agric., no. 152, 16 pp.

SQUIRE, F. A. (1940). Observations on the larval diapause of the Pink Bollworm, *Platyedra gossypiella*, Saund.—Bull. ent. Res., **30**, pp. 475–481.

STEARNS, L. A. (1921). The life-history of the Oriental Fruit Moth in northern Virginia.—Tech. Bull. Va agric. Exp. Sta., no. 21, 46 pp.

STEARNS, L. A. & NEISWANDER, R. B. (1930). Oriental Fruit Moth investigations in Ohio. I.—Bull. Ohio agric. Exp. Sta., no. 457, 36 pp.

STEARNS, L. A. & PETERSON, A. (1928). The seasonal life history of the Oriental Fruit Moth in New Jersey during 1924, 1925 and 1926.—Bull. N.J. agric. Exp. Sta., no. 455, 48 pp.

UVAROV, B. P. (1931). Insects and climate.—Trans. ent. Soc. Lond., **79**, pp. 1–247.

WOOD, W. B. & SELKREGG, E. R. (1918). Further notes on *Laspeyresia molesta*.—J. agric. Res., **13**, pp. 59–72.

THE *LEUCOPTERA* LEAF MINERS OF COFFEE ON KILIMANJARO.

II.—*LEUCOPTERA CAFFEINA* WSHBN.

By F. B. Notley, M.Sc., A.I.C.T.A., F.R.E.S.

In a previous paper (Notley, 1948), notes on *Leucoptera coffeella* (Guér.) were given. The present paper deals with the species *Leucoptera caffeina* Wshbn. This insect causes considerable damage on occasion in the coffee plantations of Kilimanjaro, in Tanganyika, and is particularly apt to occur epidemically in the Uru district, usually in the closing months of the year. Its distribution, so far as this is known, is given in the paper cited above. For the completion of records, figs. 1, 2 and 3 give the rainfall, screen temperatures, and relative humidity recorded at the Coffee Research Station, Lyamungu, for the period over which the work on leaf miners was done.

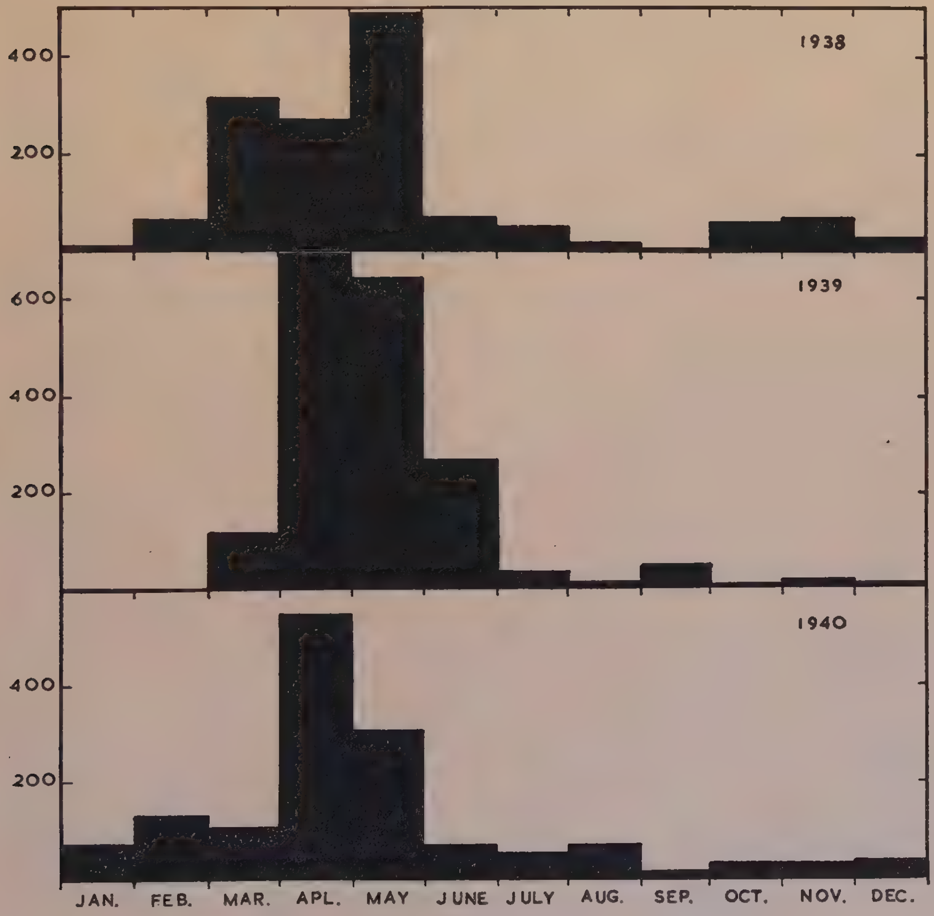


Fig. 1.—Rainfall (mm.), Coffee Research Station, Lyamungu.

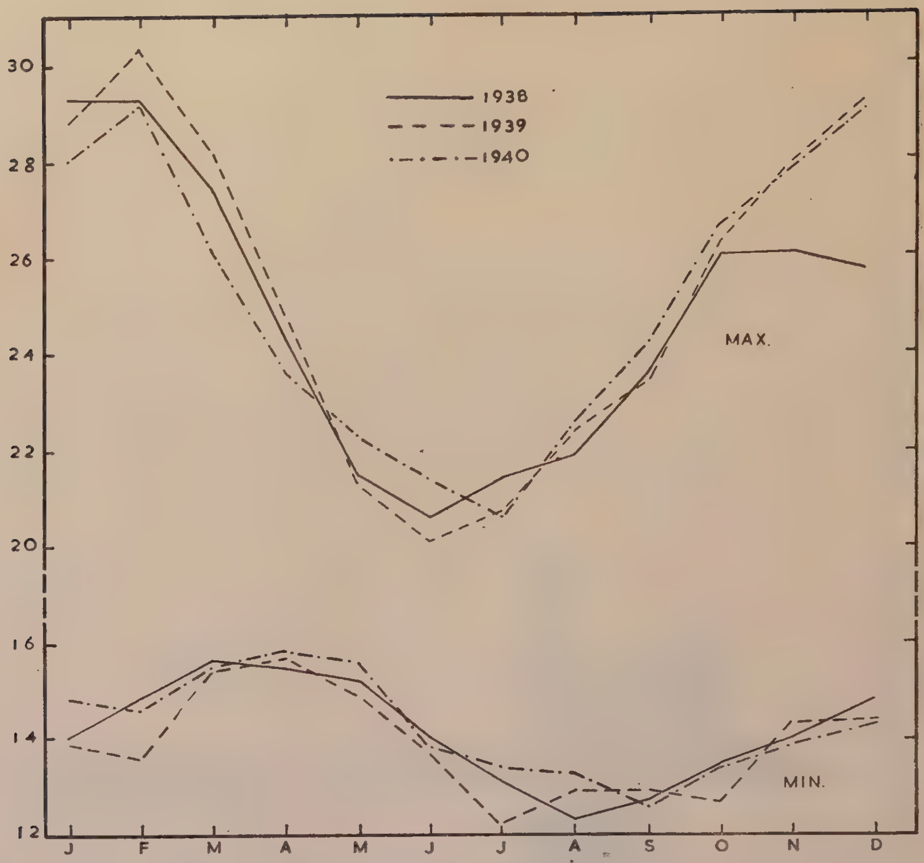


Fig. 2.—Monthly mean screen temperatures, Coffee Research Station, Lyamungu.

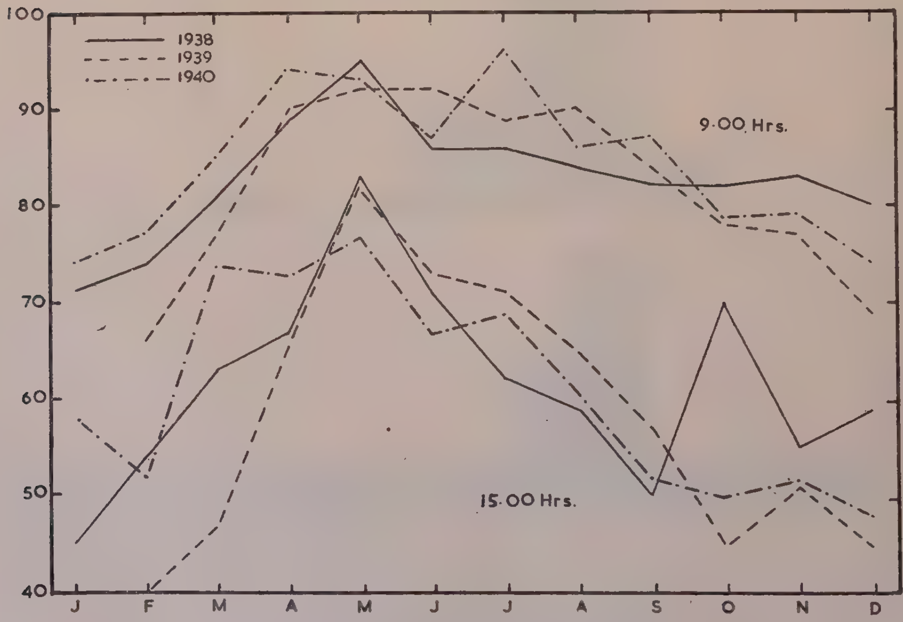


Fig. 3.—Monthly mean relative humidity per cent., 0900 and 1500 hours, Coffee Research Station, Lyamungu.

Bionomics.

The adult was described by Washbourn (1940). In the field, the mines of *L. caffeina* may be easily distinguished from those of *L. coffeella* by the arrangement of the eggs, which adhere well to the leaf and may therefore be found even after the larvae have left it and pupated. The eggs are laid in a row on the upper surface of the leaf, invariably against the midrib or a large secondary vein, with their long axes at right angles to the vein. Very occasionally more than one row is laid. The eggs of *L. coffeella* are scattered in small groups on the upper surface of the leaf, are not adjacent to each other, and are oriented at random (fig. 4).

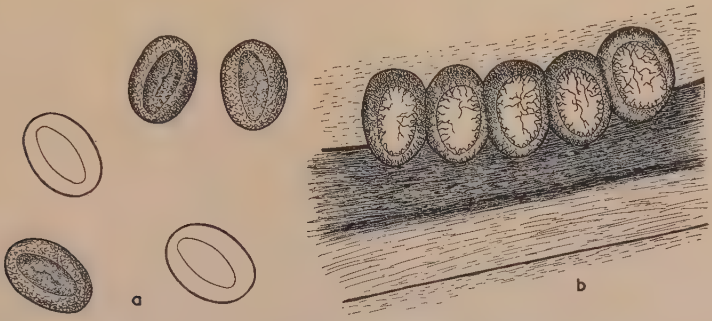


Fig. 4.—Eggs of (a) *L. coffeella* and (b) *L. caffeina* (× 39).

T. W. Kirkpatrick found that the number of eggs per batch laid by wild adults at Amani was from one to 13, with a mode and average of five, but for adults bred in the laboratory the mode was four and the average 3·6. This average was rather variable. At Lyamungu, in the field, the average number per batch varied from 5·5 to 6·1, with extremes of one and 13.

The young larvae eat their way through the epidermis of the leaf immediately below the egg, and then usually in a straight line at right angles to the vein for the first 3–5 days, when the mine is usually about 20–25 mm. long. All the eggs hatch at the same time, and at first the larvae feed together in a row. Usually some at least of them feed together throughout larval life. The excreta are pasted on the underside of the upper epidermis, as in *L. coffeella*.

The leaf-area mined by each larva is about 130 sq. mm. (range 87–157 sq. mm.). If the mine is near the base of the leaf and fairly large, the whole leaf is shed. In an outbreak at Uru in 1946 it was estimated that the number of larvae present was sufficient to consume more than the total leaf surface of the trees, and in fact almost total defoliation occurred.

There are four larval instars. No simple method of distinguishing between larvae of *L. caffeina* and *L. coffeella* is known, but as mentioned, their mines can easily be distinguished by the arrangement of the eggs. In mixed infestations, which are the rule rather than the exception, mines of *L. coffeella* may occasionally coalesce with those of *L. caffeina*, and the two species continue to develop in the same mines. It is then not possible to distinguish the larvae, until they pupate, except by the mandibles of the last instar: those of *L. caffeina* have three marked teeth and a slight molar protuberance, while those of *L. coffeella* have two teeth and a slightly more pronounced molar protuberance (fig. 5).

When ready to pupate, the larvae open semilunar holes at the edge of the mine and escape. They usually affix a strand of silk to the leaf and then drop by it either to lower leaves or to the ground, so that cocoons are found on lower leaves, or on weeds and fallen leaves on the ground. This habit is much more marked with *L. caffeina* than *L. coffeella*, which, though it has the same habit, does not drop so far, and is only rarely found pupating on fallen leaves. Thus, in mixed infestations, pupae collected from fallen leaves are almost entirely those of *L. caffeina*, while of those collected on the tree a large proportion are *L. coffeella*.

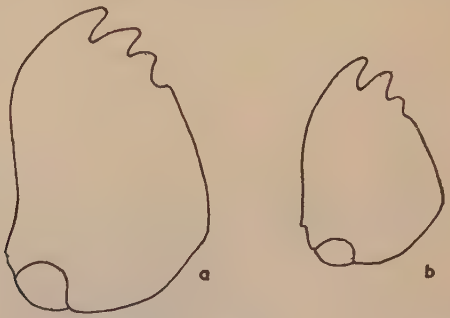


Fig. 5.—Mandible of last-stage larva of (a) *L. caffeina* and (b) *L. coffeella*.

The cocoon is spun exactly as in *L. coffeella*. First, a series of strands are spun in two arcs, joined tangentially to form a cover shaped like a tall, narrow "X". Under the junction of these arcs the larva then spins a spindle-shaped cocoon, within which it pupates. The larval exuvium is extruded from the end of this cocoon, and may remain *in situ* or fall out altogether. The cocoons are

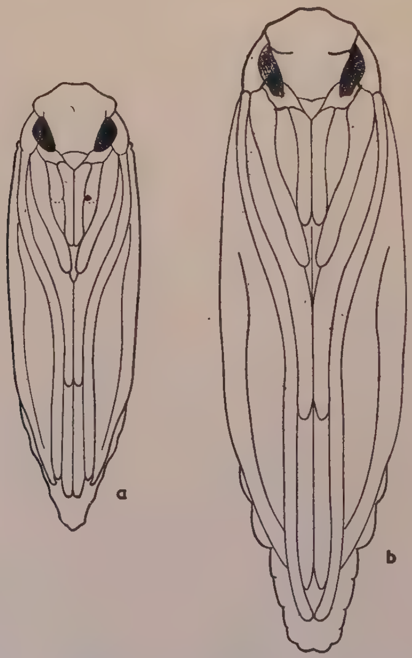


Fig. 6.—Ventral view of pupa of (a) *L. coffeella* and (b) *L. caffeina* (× 23).

difficult to distinguish from those of *L. coffeella*, but are usually rather larger. The pupae may be easily distinguished, since in *L. caffeina* the antennae project beyond the third legs, whilst in *L. coffeella* the third legs project slightly beyond the antennae (fig. 6).

The male and female adults may be distinguished by the shape of the terminal segments (fig. 7). The adults mostly emerge between 0600 and 0800 hours, though some may emerge up to 1500 hours, and the number of males and females is approximately equal. Copulation was not observed, and must take place at night. In the laboratory the adults are rather short lived, averaging only 4·7 days; very few lived more than seven days. Eggs are laid the first night after emergence. The maximum number of eggs laid in one night was 54, but the average was only 16·0. Many females did not lay at all; for those which did, the average number of eggs was 24·8 and the maximum 86. The number laid on a growing bush in a cage in the open averaged 52 per female, and it seems likely that the conditions in the laboratory were for some reason unfavourable.

The total developmental period from oviposition to emergence of the adult has been given (Notley, 1948). The durations of the various stages are as follows:—

Stage	Average temperature (°C.)	Days
Egg	24·5 24 22–21 20·5–19·5	5 6 7 7–8
Larva	24 22·5 21 19·5	13 15 19 21–23
Pupa (More variable for a given temperature than *L. coffeella*) ..	 22·5–22 20–19	♂♂ ♀♀ 5½–7 5–6½ 9–13 8–10
Total life-cycle, egg to emergence of adult (approximate) ..	24 22·5 21 20 19·5–19	25 28 33 32–36 37–41

All species of coffee appear to be attacked, but *L. caffeina* only appears to thrive on *Coffea arabica*. On Kilimanjaro it has been recorded from *C. canephora*, *C. arabica* var. *erecta*, *C. canephora* var. *robusta*, *C. congensis*, *C. eugenioides*, *C. arabica* var. *maragogype*, *C. canephora* var. *Quillou* and *C. excelsa*. Kirkpatrick (*in litt.*) records *Tricalysia* sp. as an alternative host, and Ritchie (1936) records *Pavetta oliveriana* and *P. ternifolia* in Bukoba, as alternative hosts.

There appear to be very few eggs that fail to hatch in the field; Kirkpatrick found that 72 per cent. of eggs laid in the laboratory hatched. At times, however, there appears to be a high mortality amongst first-instar larvae, the cause of which is unknown.

The mortality amongst older larvae is small, and amongst pupae practically nil, except for parasitism. Notes on the bionomics of parasites of *L. coffeella* and *L. caffeina* have already been given (Notley, 1948). It is noteworthy that whilst *Apanteles bordagei* Giard is a parasite of *L. coffeella* alone, there is no parasite which is peculiar to *L. caffeina*. The remaining parasites are common to both *L. coffeella* and *L. caffeina*.

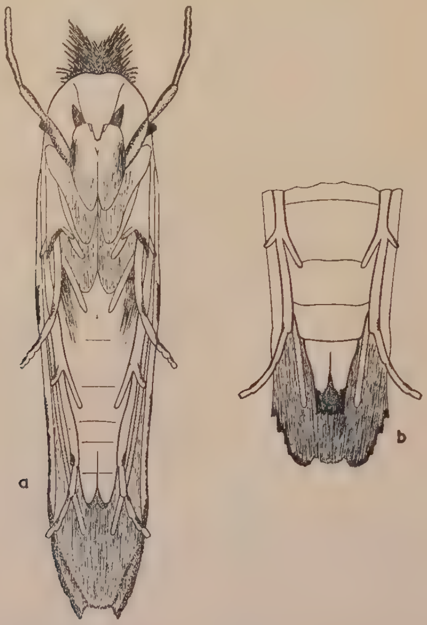


Fig. 7.—*L. caffeina*: ventral view of (a) male and (b) apex of female (× 19).

Population Studies on *L. caffeina.*

Population studies of *L. caffeina* and its parasites were made in the field at the Coffee Research Station, on Kilimanjaro, during the years 1937–40, in both shaded and unshaded coffee.

Unshaded coffee.

|rs

There is little of value on record on *L. caffeina* in unshaded coffee, where it is comparatively rare, and confined to leaves in the centre of the tree, which are naturally shaded by the outside leaves. The number of eggs per tree from June 1938 to December 1940 are shown in fig. 8. If these figures are compared with those given for *L. coffeella* over the same period on the same trees (Notley, *op. cit.*, fig. 3), it will be seen that nearly every rise in the number of eggs of *L. coffeella* was accompanied by a similar rise in those of *L. caffeina*. The figures for parasitism, however, were small and extremely variable, and it is suggested that the increases are due to causes other than the failure of parasites. It seems possible that the great increase in eggs of *L. coffeella* in 1938, rising to over 1,700 per tree, would have offered parasites more hosts than they could attack, and thus given the eggs of *L. caffeina* a greater chance of escape than they would have had alone. The rise in numbers in 1939, however, which took place although there was only a comparatively small rise in numbers of *L. coffeella*, may have been due to continued invasion of the unshaded coffee by adults of *L. caffeina* which were breeding very rapidly at that time in the adjoining shaded coffee: the two plots on which the studies were made are only about 200 yd. apart. The figures for parasitism for *L. caffeina* in unshaded coffee give no clue to the reasons for fluctuations in numbers, and therefore these explanations are put forward with great reserve. It may be that climatic causes, as yet unknown, are responsible.

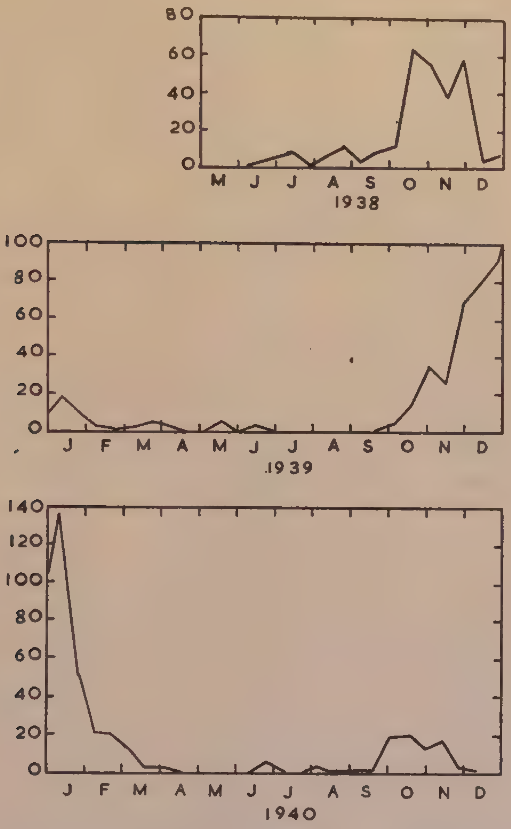


Fig. 8.—Unshaded coffee. Number of eggs of *L. caffeina* per tree, 1938–40.

Shaded coffee.

The number of eggs per tree for shaded coffee are given in fig. 9. It will be /rs noted that outbreaks of varying intensity occurred towards the end of each of the three years; in the largest of these (1939) the number of eggs per tree laid in a single fortnight reached over 3,200, practically twice that recorded for *L. coffeella* in unshaded coffee in the previous year.

The defoliation caused by this outbreak was severe, although less so than an outbreak seen by the author in 1946 at Uru. The normal life of a coffee leaf on the tree is about 9½ months (Rayner, 1950). It is recognised that bordeaux spraying increases the crop, and this is attributed to the increase of the average life of the leaf to nearly 12 months by the suppression of leaf diseases. The effect of defoliation by leaf miner on the crop has not been estimated; since there is no method known of controlling the leaf miner, it is not possible to arrange for an experiment with comparable controls to determine this point, but the loss of crop must be severe. It has been observed that trees defoliated in November–December, if the rains are adequate, can develop new leaves and flower in March, and subsequently set a good crop; but what is required to be known is whether, as seems obvious, the trees would have set a better crop had this defoliation not taken place.

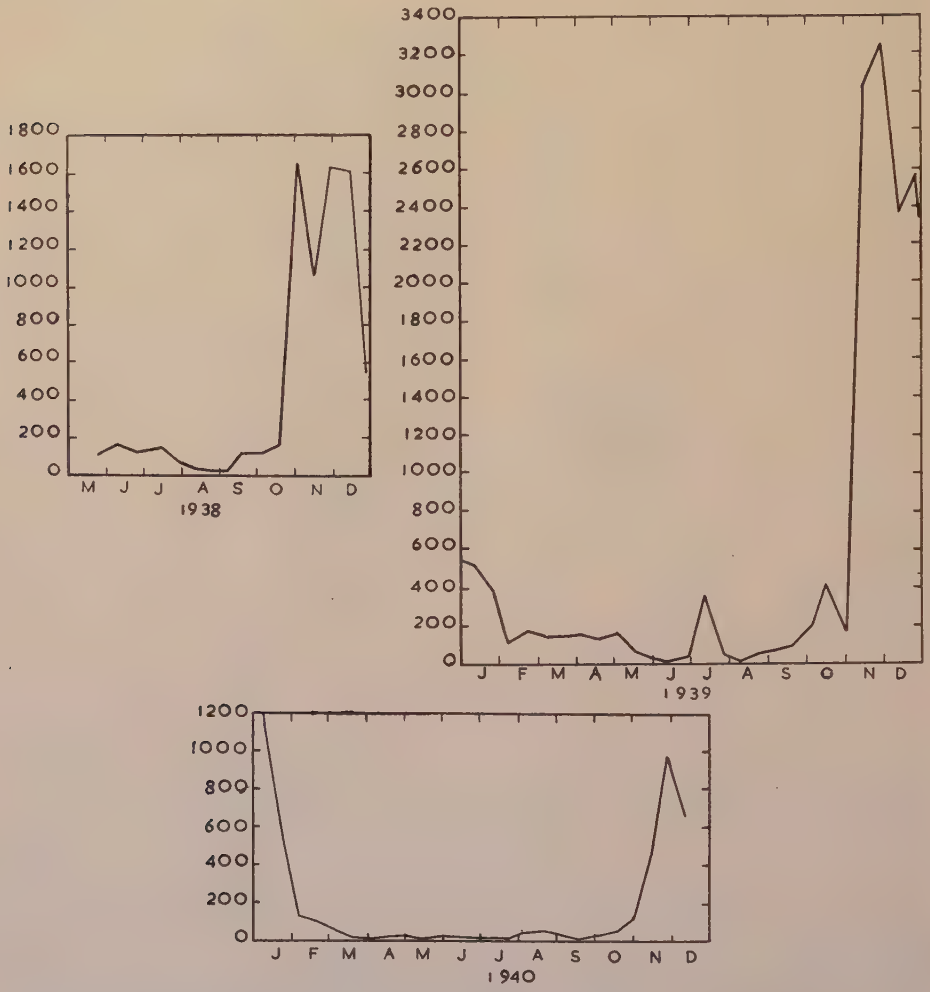


Fig. 9.—Shaded coffee. Number of eggs of *L. caffeina* per tree, 1938–40.

Egg parasites.

No egg parasites were recorded.

Larval parasites.

The mined leaves which were collected for egg-counts were placed in parasite-emergence boxes, and all adults emerging, both host and parasite, were recorded.

The species composition of the adults emerging, expressed as percentages, is shown in fig. 10 (a few *L. coffeella* and *A. bordagei*, which should not have been included in the collections, are ignored).

It will be observed that the proportion of *L. caffeina* escaping parasitism approaches 100 per cent. for a period between April and October each year. This period started latest (mid-June) in 1939, the year when the number of eggs reached its highest peak.

The only parasites emerging in large numbers were *Pleurotropis coffeicola* Ferrière and *Ageniaspis* sp., and these numbers tend to rise at the end of each year. In November 1938, *P. coffeicola* appeared to bring a small, mild outbreak under control and afterwards to maintain a balance with the host, with little help from *Ageniaspis*, until May–June 1939, when a sudden change took place and the parasites almost completely disappeared. Sustained increase in parasitism did not occur until September–October 1939 just before the greatest number of host larvae appeared (November) and was continued until the end of January 1940, by which time the host was under control. A peak of *Ageniaspis* occurred in January, followed by one of *P. coffeicola*, while the percentage of the host escaping parasitism rose steadily until, in April, practically all were escaping parasitism. A criticism may be made that by the method of collection only rather young larvae were obtained, and possibly a more accurate picture may be obtained from the pupal collections (see below). In 1940, parasites were similarly almost absent until October, when *Ageniaspis* and *P. coffeicola* again started to

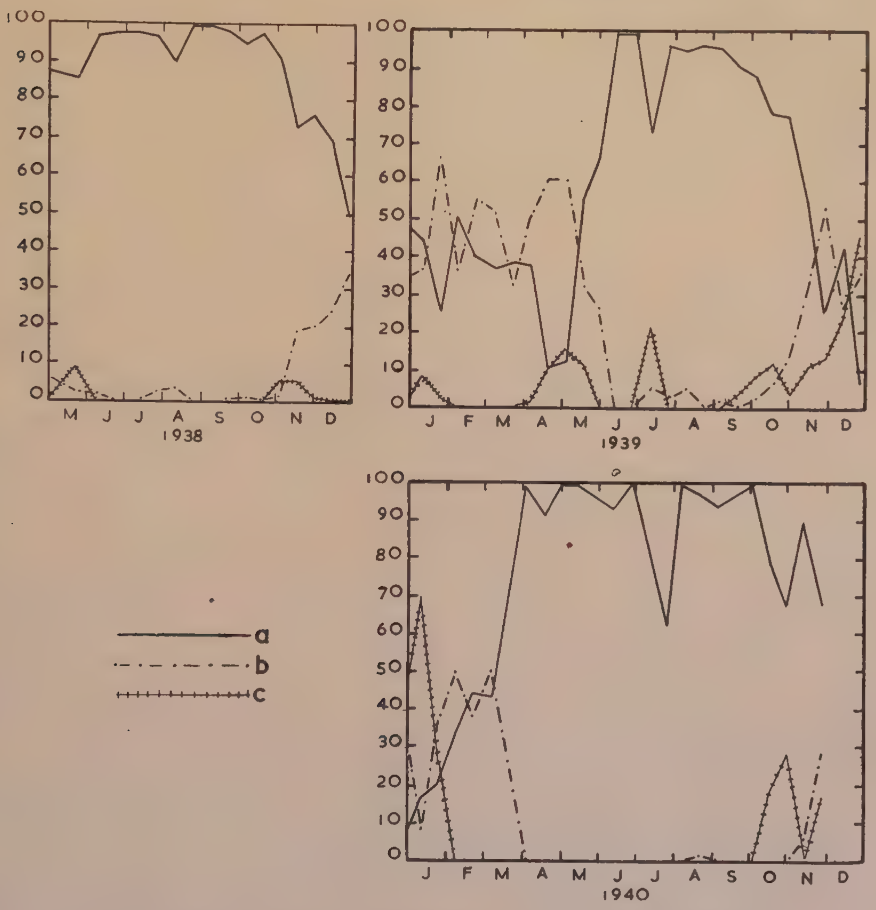


Fig. 10.—Shaded coffee. Percentage composition of emergences of adults from collections of larvae of *L. caffeina*: (a) *L. caffeina*, (b) *Pleurotropis coffeicola*, (c) *Ageniaspis* sp.

influence the position; at this point unfortunately, the work had to be closed down. The drop in July 1940 in the percentage of *L. caffeina* escaping parasitism was due to a very small total collection in which there were a few *Elasmus leucopterae* Ferrière, and might be regarded as unimportant, except as it bears on the dominant-stage theory elaborated below.

Pupal parasites.

The pupal collections give a clearer picture of total parasitism than do the larval collections. The two important parasites obtained from larval collections, *P. coffeicola* and *Ageniaspis* sp., when acting as primary parasites, allow the host to pupate, and thus appear in the emergences from pupal collections. Two other parasites also appear in numbers, *Eulophus borboricus* Giard and one determined as belonging to a new genus, near *Hormius* and hereafter referred to as "*Hormius*". Both these are primary endoparasites and attack larvae just before or just after pupation. The percentage parasitism is shown in figs. 11 and 12; data for 1939 and 1940 only are available, and from early March to early June 1940 the numbers collected were too small to justify calculation of percentages.

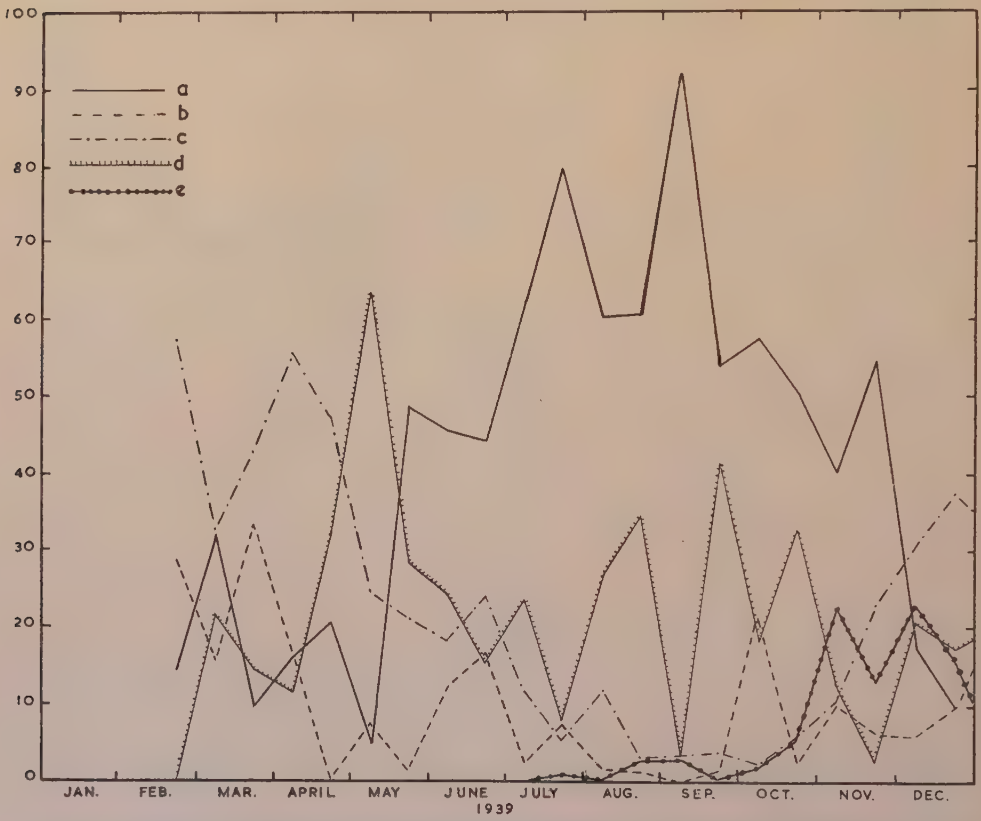


Fig. 11.—Shaded coffee (1939). Percentage composition of emergences of adults from collections of pupae of *L. caffeina*: (a) *L. caffeina*, (b) "*Hormius*", (c) *P. coffeicola*, (d) *Ageniaspis* sp., (e) *E. borboricus*.

The same tendencies for pupal parasitism as for larval parasitism may be seen, namely a large proportion of the hosts escaping parasitism from late May to late

November 1939, and from early March to October 1940. The tendency, however, does not appear to be so extreme as in the larval collections. There is a marked tendency to fluctuations in the proportions of host and parasites, and even more marked fluctuations between the parasites. During the early part of 1939, when the host was under control, parasitism was taken over from *P. coffeicola* and "*Hormius*" by *Ageniaspis*, which became the dominant parasite in the period immediately preceding the great increase in host numbers and showed large fluctuations with the host. When epidemic numbers of the host had been achieved, first *E. borboricus*, then *P. coffeicola* and finally "*Hormius*" began to increase, *P. coffeicola* becoming dominant, probably owing to its ability to attack either the host or *E. borboricus*. Finally, in late February 1940, *Ageniaspis* became dominant and *P. coffeicola* almost disappeared. Thereafter the proportion of hosts escaping parasitism immediately rose, and was still at a high level when pupae were present in reasonable numbers again in June 1940. A similar sequence occurred thereafter, namely a series of fluctuations between the host, *P. coffeicola*, *Ageniaspis* and "*Hormius*", but at the end of November 1940, when the smaller number of hosts escaping parasitism indicated that the outbreak (which was a small one) was coming to an end, "*Hormius*", *E. borboricus* and *Ageniaspis* were all prominent, while *P. coffeicola* was rather unimportant.

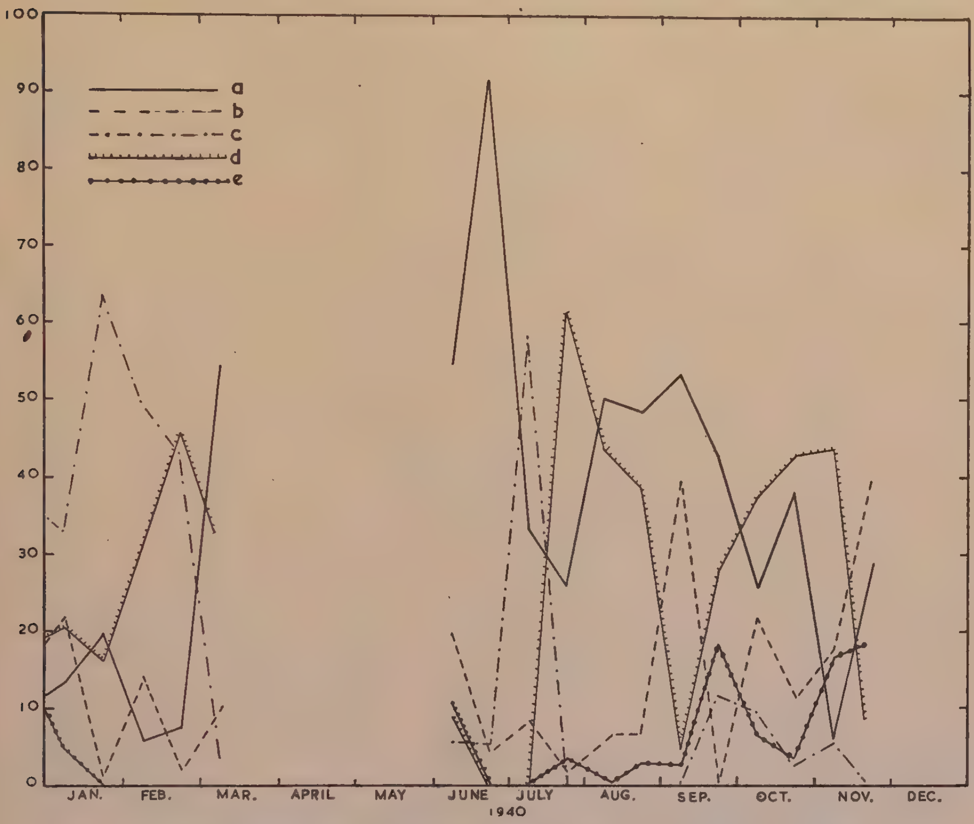


Fig. 12.—Shaded coffee (1940). Percentage composition of emergences of adults from collections of pupae of *L. caffeina*: (a) *L. caffeina*, (b) "*Hormius*", (c) *P. coffeicola*, (d) *Ageniaspis* sp., (e) *E. borboricus*.

Occurrence of the dominant stage.

The method of graphing the daily emergence, used in the previous paper to demonstrate the existence of the dominant stage in *L. coffeella* (Notley, 1948) did not show clear-cut results with *L. caffeina*. This is the more curious in that the dominant stage is often obvious in the field: there are times during an outbreak when great numbers of moths are seen in the coffee, followed by times when few moths are seen, but many mines. It seems probable that larvae of *L. caffeina* do not complete their development easily in leaves removed from the tree and placed in parasite-emergence boxes. The number of eggs per tree in 1939, the year of the largest outbreak, appear to show some signs of the fluctuation one would expect if the dominant stage were present; this is more clearly demonstrated if the figures are converted to logarithms, as in fig. 13.

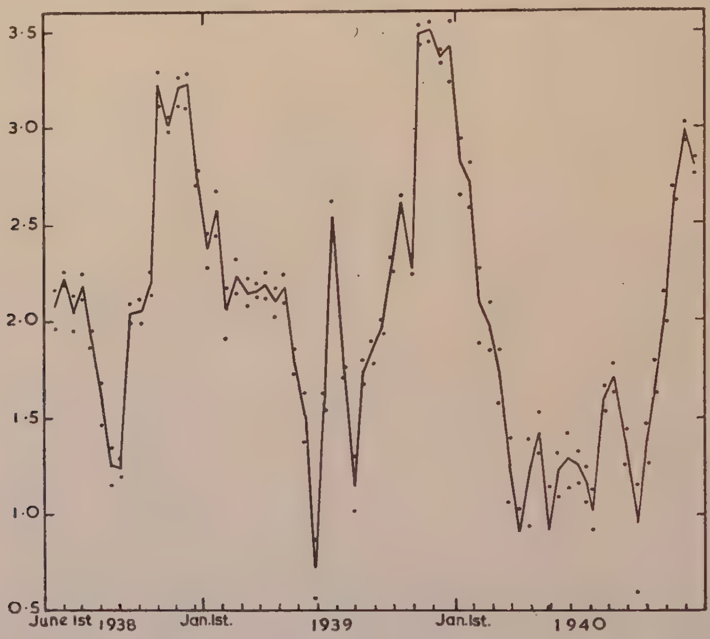


Fig. 13.—Shaded coffee. Logarithm of egg-counts of *L. caffeina* with S.E.

An even clearer picture is shown in fig. 14, which is a graph of the total number of adult insects emerging from collections of pupae made, after the first few months, at intervals of three or four days. The object in mind when the collections were made was purely to determine the percentage parasitism, and pupae were therefore collected until a reasonable number was obtained. This was usually about one hundred, except at times when the host was rare. When collecting, however, it is not possible to tell whether or not the adults have emerged from the cocoons. The fluctuations in the graph therefore indicate that at times a very high proportion, and at others a very low proportion, of the cocoons contained only empty pupal skins. The upper line in fig. 14 gives the total of adult hosts and parasites emerging from these cocoons, with the number of *Ageniaspis* adults divided by three, since this is about the average number of *Ageniaspis* derived from one leaf miner pupa. This upper line therefore indicates the total number of live hosts present, whether parasitised or not.

It can be seen that large fluctuations in numbers occur, the time between peaks being approximately that of one generation of *L. caffeina*. It is difficult to suggest any explanation of this phenomenon other than that the population of *L. caffeina* during this outbreak existed in what has been described as the dominant stage, similar to, if not so extreme as, the "one stage" condition described by Taylor (1937) as the cause of outbreaks of *Promecotheca reichei* Baly.

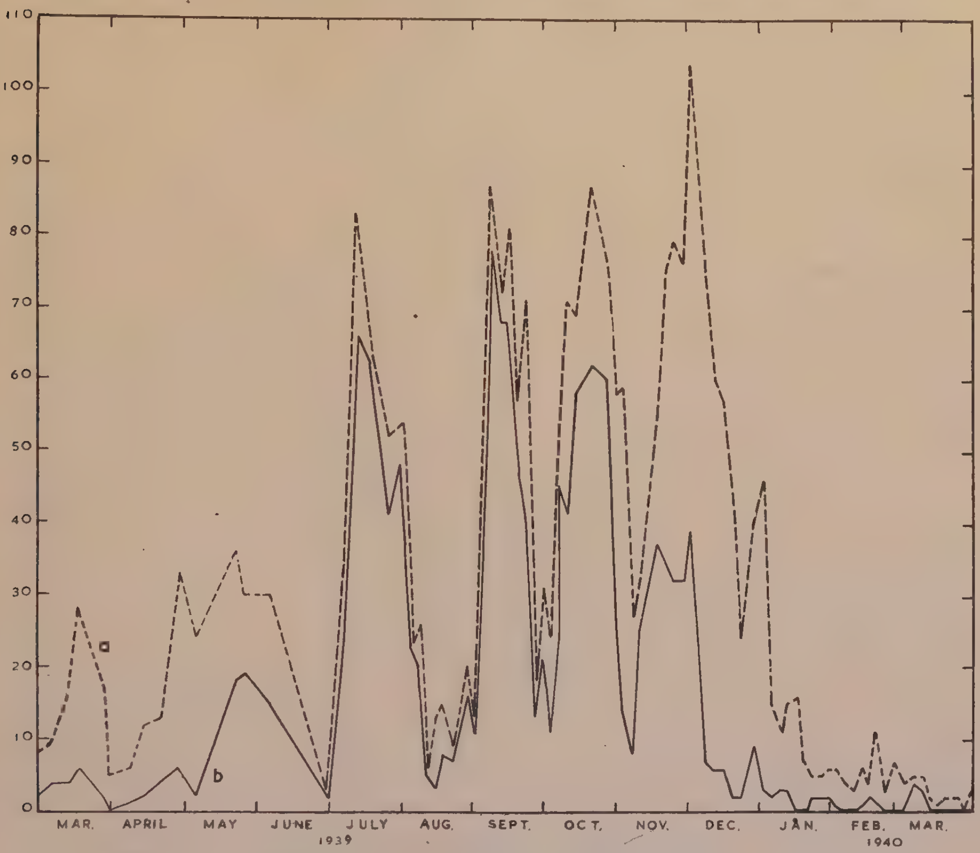


Fig. 14.—Emergences of adult insects from samples of pupae of *L. caffeina*: (a) total hosts and parasites (*Ageniaspis* ÷ 3), (b) hosts only.

Summary.

A description is given of the bionomics of *Leucoptera caffeina* Wshbn. in the Kilimanjaro District, Tanganyika, and of the characters that distinguish it in its various stages from *L. coffeella* (Guér.), together with the results of population studies of the former insect and its parasites in both shaded and unshaded coffee in 1938–40.

During the 1939 outbreak, the numbers of eggs per tree, and the number of live pupae present in samples of about 100 cocoons (estimated from the number of moths and parasites emerging) showed large fluctuations. The times between peak numbers approximated to the total life-cycle, indicating that at any moment one developmental stage was dominant.

Acknowledgements.

Again I have to record my indebtedness to Professor T. W. Kirkpatrick, now of the Imperial College of Tropical Agriculture, Trinidad, for generously placing

at my disposal all his notes and drawings on leaf miner made when he was at the East African Agricultural Research Station, Amani,* and also to the Commonwealth Institute of Entomology, for the identification of specimens.

References.

NOTLEY, F. B. (1948). Bull. ent. Res., **39**, pp. 399–416.

RAYNER, R. W. (1950). Rep. Dep. Agric. Kenya, 1948, p. 146.

RITCHIE, A. H. (1936). Rep. Dep. Agric. Tanganyika, 1935, p. 97.

TAYLOR, T. H. C. (1937). The biological control of an insect in Fiji.—239 pp. London, Imp. Inst. Ent.

WASHBOURN, R. (1940). Bull. ent. Res., **30**, pp. 455–462.

---

* Figs. 4, 6 and 7 are his drawings, and a great number of his observations have been included here.

STUDIES ON THE CHEMICAL CONTROL OF WIREWORMS (*AGRIOTES* SPP.).

I.—THE DIRECT AND RESIDUAL EFFECTS OF BHC, DDT, D-D, AND ETHYLENE DIBROMIDE.

By C. Potter, M. J. R. Healy and F. Raw
Rothamsted Experimental Station, Harpenden, Herts.

(Plates XXIII & XXIV.)

Wireworms are important pests in Great Britain, and a considerable amount of research work has been devoted to them. Some of the more recent British work is summarised by Thomas (1949), and reviews of work in other countries are given by Lange (1947) and Ernould (1948).

Benzene hexachloride has been used to a great extent in this country to control wireworms and detailed experiments with it are described by Jameson, Thomas & Woodward (1947) and Jameson, Thomas & Tanner (1951). The latter publication describes its use when applied as a seed dressing of cereals. Golightly (1946) gave data to show that DDT could reduce wireworm attack and this was confirmed by Jameson, Thomas & Woodward (1947).

While workers abroad have found BHC effective for wireworm control on a wide range of crops, under varying experimental conditions and with a number of species of wireworm, DDT has been found to be relatively ineffective by some workers (Arnason, Fox & Glen, 1948; Pepper, Reed & Campbell, 1949; Blanka, 1950; Galakhov, 1950; Ingram & others, 1950). Other workers, however, have obtained good results with DDT (Roberts, 1947; Lane & others, 1948; Anon., 1949; Stone & Foley, 1954).

Soil fumigation for wireworm control has not been used to any extent in England, but has been found to give good results under some conditions abroad. The fumigants mainly used for this purpose are ethylene dibromide and D-D (Lange, 1945; King, Arnason & Manson, 1948; Cook, 1949; Pepper, Reed & Campbell, 1949; Stone, 1949; Stone & Foley, 1954).

In the spring of 1947 a crop of winter wheat in Little Hoos Field, Rothamsted, was severely damaged by wireworms of the genus *Agriotes*. Sampling showed that the wireworm population was about 1·25 million per acre. The following autumn, two experiments were laid down which were continued for four years. The soil was heavy clay with flints.

The experiments were designed to compare the effects of BHC, DDT, ethylene dibromide and D-D, when applied under similar conditions to control wireworms.

Since very few data were available on the after-effects of a single treatment, the experiments were continued over a period of four years to determine the effect of the various treatments on infestation of succeeding crops. Since it was known that BHC might cause taint, some experiments to determine the risk of taint by this insecticide were included.

Experiment I, 1947–51.

The treatments, applied in October 1947, were as follows:—

BHC seed dressing—	seed treated at the rate of 2 oz./bushel with a dressing containing 20 per cent. technical γ isomer.

BHC combine-drilled—	3·5 per cent. wireworm dust combine-drilled with the seed at $\frac{3}{4}$ cwt./acre giving 2·9 lb./acre crude BHC $\equiv$ 5·7–6·0 oz. γ isomer per acre.
BHC broadcast—	3·5 per cent. wireworm dust broadcast immediately before sowing at 2 cwt./acre giving 7·9 lb./acre crude BHC $\equiv$ 15·2–16·0 oz. γ isomer per acre.
DDT combine-drilled—	5 per cent. DDT dust combine-drilled with the seed at 144 lb./acre giving 7·2 lb./acre technical DDT.
D-D (a liquid product consisting essentially of a number of isomeric dichloropropenes, together with 1,2-dichloropropane and other chlorinated hydrocarbons. The chief component of the mixture is 1,3-dichloropropene.)	A mixture containing D-D and tractor vapourising oil in equal volumes injected 6 in. deep 19 days before sowing at the rate of 210 lb./acre D-D.
Ethylene dibromide—	A mixture containing 20 per cent. by volume technically pure ethylene dibromide and 80 per cent. by volume tractor vapourising oil injected 6 in. deep 19 days before sowing at the rate of 45·5 lb./acre ethylene dibromide.
Controls—	No treatment.

Methods.

Recognised practice was followed for the solid insecticides which were applied by broadcasting, combine-drilling and seed dressing.

The soil fumigants were applied by means of a special injector loaned by courtesy of the Shell Company. This machine consists of a reservoir, a motor and six injector tubes, each tube attached behind a special tine of the cultivator type. The rate of flow of the fumigant and hence the rate of application for a given tractor speed can be adjusted. The whole machine is mounted on pneumatic tyres and is tractor-drawn. Some details of this machine are given by Grainger (1951) under the heading " An American Prototype Injector ". In these experiments, the tines were set 9 in. apart and set to deliver the fumigant at 6 in. depth. The tines drilled a furrow and volatile liquids dribbled through the tubes into the furrows. Immediately after each fumigant had been applied to the test plots, they were rolled to consolidate the surface.

There seems to be no evidence that the conditions at the time of treatment affect the action of the solid insecticides, but a number of workers (Newhall, 1946; King, Arnason & Manson, 1948; Cook, 1949; McClellan, Christie & Horn, 1949; Stone, 1949) have shown that temperature and soil conditions may greatly affect the action of the fumigants. Records of the prevailing conditions on the day of application were therefore taken. The weather was dull and cloudy with a S.W. wind, $15\frac{2}{3}$ ft./sec. at two metres high and 14 ft./sec. one metre high at the beginning of fumigant application and $14\frac{1}{3}$ ft./sec. at two metres and $11\frac{3}{5}$ ft./sec. at one metre at the end of the experiment. The air temperature at the surface of the soil was 16·5°C.; the soil temperature 6 in. deep was 12·5°C. The ground was clay with flints that had been harrowed down to seed-bed consistency.

At the time the experiments were started there was very little information on which materials were most economical when applied at their effective dosage rates. Dosage rates were chosen which, judged from the literature, would prove effective.

The experiment was laid out as three randomised blocks of nine plots (one for each treatment and three controls), each plot being 14 × 90 ft. (0·0289 acre). The experiment was continued for four years without further application of the treatments except that in the final year, 1951, the plots which had originally received BHC seed dressing were used for another experiment. The wheat variety was Bersee in 1948 and 1949, Squareheads Master (13/4) in 1950, and Nord Desprez in 1951, sown at 3 bushels/acre.

Effect of treatments on yield.

The direct effect of each treatment was assessed by the yield of grain and straw at harvest in 1948 and the residual effect by the yield in 1949, 1950 and 1951. These results are given in Table I.

TABLE I.

The direct and residual effects of a single treatment with different insecticides on yield of grain and straw.

	Yield of grain (cwt. per acre)								
	Controls	BHC			DDT	D-D	Ethylene dibromide	Standard errors	
		Seed dressing	Combine-drilled	Broad-cast				Controls	Others
1948	8·9	24·0*	24·8*	30·6*	20·7*	28·3*	32·1*	0·87	1·51
1949	28·4	24·2	37·3*	39·6*	36·4*	31·8*	34·1*	0·77	1·33
1950	15·5	11·7	15·0	16·1	18·0	16·9	18·8*	0·72	1·25
1951	14·7	—	16·5	17·2	20·3*	15·6	15·5	0·84	1·18
	Yield of straw (cwt. per acre)								
1948	22·8	54·6*	54·2*	65·9*	46·0*	64·1*	71·6*	2·12	3·68
1949	33·5	28·5	42·2*	46·1*	41·5	35·8	37·4*	0·89	1·54
1950	25·0	20·9	23·0	25·8	27·1	27·0	27·8	1·09	1·88
1951	16·3	—	18·0	18·9*	20·1*	17·8	17·8	0·72	1·02

* Values which significantly exceed the controls ($P < 0{\cdot}05$).

In the year of application all the treatments resulted in a marked increase in yield of grain and straw. BHC broadcast and the soil fumigants gave the best results followed by BHC seed dressing and BHC combine-drilled. DDT was the least effective, though even here the yield of both grain and straw was more than twice that of the control plots.

In the following year when wireworm damage, as judged by the yield of the control plots, was much less, the BHC seed dressing showed no residual effect. BHC combine-drilled, BHC broadcast and DDT showed a substantial residual effect. The soil fumigants, especially D-D, were somewhat less effective.

In subsequent years residual effects were less marked, though ethylene dibromide showed a significant effect in 1950 and BHC broadcast and DDT in 1951.

Effect on plant growth.

In the spring of 1948 and 1949, estimates of plant height and density were made. Four one-yard lengths of drill were chosen at random in each plot, and the number of plants and the heights of three plants in each yard were recorded. The results are given in Table II.

TABLE II.

Effect of treatments in the year of application and the year following application on plant density and height of wheat plants.

Plant numbers (thousands per acre)

Date	Controls	BHC			DDT	D-D	Ethylene dibromide	Standard errors	
		Seed dressing	Combine-drilled	Broad-cast				controls	others
1.iii.48	1170	1327*	1095	1322*	1247	1317*	1357*	34	59
13.iv.48	465	1021*	804*	1250*	801*	1197*	1678*	56	98
10.v.49	1240	1068	1477	1744*	1545*	1489*	1390	61	105

Plant height (in in.)

Date	Controls	BHC Seed dressing	BHC Combine-drilled	BHC Broad-cast	DDT	D-D	Ethylene dibromide	Standard errors controls	Standard errors others
1.iii.48	3·10	3·01	2·98	2·99	3·14	3·07	3·07	0·06	0·10
13.iv.48	4·56	5·35*	4·83	5·51*	5·04	5·92*	5·93*	0·13	0·22
10.v.49	11·2	10·9	12·4*	12·6*	12·4*	11·4	11·7	0·26	0·44

* Values which significantly exceed those of the controls ($P < 0{\cdot}05$).

These results agree with those in Table I. By mid-April 1948, when wireworm damage had severely thinned the control plots, all the treated plots carried a much denser stand of wheat accompanied by better growth on plots treated with BHC seed dressing, BHC broadcast, D-D and ethylene dibromide (see Pl. XXIII, figs. 1–4, & XXIV, fig. 1).

In 1949 there was a residual effect on the plots previously treated with BHC combine-drilled, BHC broadcast, DDT and D-D.

TABLE III.

Effect of treatments in 1948 on the wireworm population assessed in 1950.

Total wireworm counts,* September 1950.

Year-group	Controls	BHC			DDT	D-D	Ethylene dibromide	Total
		Seed dressing	Combine-drilled	Broad-cast				
1st ..	25	3	11	0	4	18	6	67
2nd ..	63	21	3	3	3	16	8	117
3rd ..	24	17	7	1	4	14	4	71
4th ..	11	6	3	0	1	1	2	24
Total ..	123	47	24	4	12	49	20	279
% in top 6 in.	74	77	75	50	75	84	60	

* Controls, 9 plots; others, 3 plots.

Effect on the wireworm population.

The plots were sampled for wireworms in September 1950. Four random soil samples each 4 in. diameter and 12 in. deep were taken from each plot, divided into an upper and lower half and the wireworms extracted by a standard flotation method. The length of each wireworm when fully extended was measured and on the basis of the size distribution of all the wireworms they were divided into four groups corresponding approximately to year groups, *i.e.*, to larvae hatched in the four years 1947–50. The results are summarised in Table III.

The counts were transformed to square roots for analysis, first including all larvae and then excluding first-year larvae, *i.e.*, those which hatched in 1950. The results are given in Table IV.

TABLE IV.

Analysis of the effect of insecticide treatments on the wireworm population.

Mean numbers of wireworms per plot (square root transformation)

	Controls	BHC			DDT	D-D	Ethylene dibromide	Standard errors	
		Seed dressing	Combine-drilled	Broad-cast				controls	others
All larvae	3·70	3·87	2·83	1·33*	2·03*	4·10	2·60*	0·25	0·43
Less 1st-year larvae	3·30	3·73	2·20*	1·33*	1·63*	3·23	2·20*	0·25	0·43

* Values significantly less than those of the controls ($P < 0{\cdot}05$).

It can be seen that, three years after application, the plots treated with BHC broadcast, DDT and ethylene dibromide had a distinctly lower wireworm population than the control plots. These three treatments had a marked residual effect on yield of grain and straw in 1949 and on either grain or straw in 1950 or 1951. If the first-year larvae are excluded, the plots treated with BHC combine-drilled also have a lower population than the control plots and this treatment also had a marked residual effect on yield in 1949. The populations of the plots treated with BHC seed dressing and D-D were very similar to that of the controls. D-D had shown a residual effect on yield of grain in 1949 though this effect was the least of those produced.

It can be seen from Table III that none of the treatments had any marked effect on the vertical distribution of the wireworms.

Experiment II, 1947–51.

The second series of treatments, applied in October 1947, were as follows:—

BHC seed dressing— (S)	Seed treated at the rate of 2 oz./bushel with a dressing containing 20 per cent. technical γ isomer.
BHC combine-drilled— (D_1, D_2, D_3)	3·5 per cent. wireworm dust combine-drilled with the seed at $\frac{1}{4}$, $\frac{1}{2}$ and 1 cwt./acre giving 0·98, 1·96 and 3·92 lb./acre crude BHC $\equiv$ 1·9–2·0 oz., 3·8–4·0 oz. and 7·6–8·0 oz. of γ isomer per acre.
Controls (O)—	No treatment.

The experiment was laid out in three replicates, each consisting of three incomplete blocks of three plots. The plot size was 14 × 90 ft. as in Experiment I. After harvest in 1948 one replicate was set aside for the experiment on tainting described below. In the remaining two replicates half the control plots and half the BHC seed-treatment plots were sown with seed treated with the BHC seed dressing. All the remaining plots were sown with untreated seed. Subsequently untreated seed was used throughout. In the fourth year some of the plots which had received the BHC seed dressing were used for another experiment. Wheat varieties and seed rates were as in Experiment I.

Effect of treatments on yield.

The yields of grain and straw are given in Table V.

TABLE V.

Direct and residual effects of different BHC treatments on the yield of grain and straw.

1947 treatments ..	0†	0	S	S	D1	D2	D3	Standard errors		
1948 treatments ..	0	S	0	S	0	0	0	1	2	3
				Grain (cwt. per acre)						
1948	13·4		26·5*		28·4*	27·5*	27·1*	0·76	1·42	1·12
1949	27·1	28·6	23·8	25·3	32·5*	35·6*	36·3*	1·07	1·37	1·23
1950	11·4	11·5	8·1	7·6	13·3	15·7	17·2*	1·47	1·88	1·69
1951	19·8	—	—	—	19·5	19·9	20·6	—	0·58	0·66
				Straw (cwt. per acre)						
1948	32·8		56·2*		60·2*	60·4*	58·0*	1·63	2·65	2·23
1949	30·1	32·6	28·4	30·7	36·6*	38·2*	40·5*	1·28	1·64	1·47
1950	18·7	19·8	14·7	13·0	20·0	22·8	24·6	2·26	2·89	2·59
1951	20·6	—	—	—	19·7	19·9	20·2	—	0·67	0·76

* Values significantly greater than the controls ($P < 0{\cdot}05$).

Standard errors 1 for comparisons O v. S v. (mean of D's)
2 ,, ,, D_1 v. D_2 v. D_3
3 ,, ,, O, S v. D_1, D_2 or D_3.

† See text for explanation of treatment symbols.

In the year of application all the treatments were effective to a similar extent. In the two subsequent years BHC combine-drilled showed a residual effect but the BHC seed dressing did not, the yields from the seed-dressed plots being less than the controls, as in Experiment I. The BHC seed dressing applied in 1948 had no detectable effect in contrast with the results from both experiments in the previous year. This may have been due to the less severe wireworm attack.

Effect on plant growth.

In the spring of 1948, estimates of plant density and height were made as in Experiment I. The results are given in Table VI.

These results agree with those in Table V. By mid-April, all the treated plots had a much denser stand of wheat than the controls, accompanied by better growth on the plots whether treated with BHC as a seed dressing or combine-drilled (see Pl. XXIV, figs. 2–4).

The effect of the treatments on the wireworm population was not investigated.

TABLE VI.

Effect of different BHC treatments on plant density and height of wheat plants.

Plant numbers (thousands per acre)								
Date	0†	S	D_1	D_2	D_3	Standard errors		
						1	2	3
1.iii.48	1125	1332*	1235	1220	1123	28	59	44
13.iv.48 ..	650	1220*	1021*	1135*	921*	56	89	76
Plant height (in in.)								
1.iii.48 ..	3·11	3·24	3·16	3·29	3·07	0·05	0·10	0·08
13.iv.48 ..	4·72	5·46*	5·62*	5·64*	5·16	0·14	0·20	0·18

* Values that significantly exceed those of the controls.

Standard errors 1 for comparisons O v. S v. (mean of D's)
2 ,, ,, D_1 v. D_2 v. D_3
3 ,, ,, O, S v. D_1, D_2 or D_3.

† See text for explanation of treatment symbols.

Tainting by BHC.

In the season 1948–49 one replicate of Experiment II was cropped with lettuces, red beet, carrots and potatoes to investigate possible tainting by the BHC treatments applied in the previous year. The test crops were sown in rows across the plots and sampled at random for tasting. Seven judges, selected from a group of volunteers after preliminary tests with aqueous dilutions of BHC were asked to award marks out of 10 for general flavour. The lettuces were tasted raw, the other vegetables were peeled or scraped and boiled. Because of

TABLE VII.

Average scores in tainting trials.
(angular transformation—90° = excellent flavour)

						Standard errors	
	0†	S	D_1	D_2	D_3	1	2
Lettuces	52	52	64	38	50	4·5	7·7
Beetroot	41	55	54	23*	34	3·6	6·2
Carrots	48	50	48	49	27*	3·4	5·9
Potatoes	71	64	55*	57*	53*	3·1	4·4

* Values significantly below the controls ($P < 0{\cdot}05$).

Standard errors 1 for comparisons O v. S
2 ,, ,, O, S v. D_1, D_2 or D_3.

† See text for explanation of treatment symbols.

drought in the growing season, the lettuces, beetroot and carrots had a strong natural flavour in all the plots and the potatoes proved the most sensitive test crop. The scores were transformed to degrees for analysis. The results are given in Table VII.

These tests show that BHC, combine-drilled at the rate of 1·96 lb./acre and above, tainted beetroot, carrots and potatoes. Potatoes were tainted when BHC was combine-drilled at the rate of 0·98 lb./acre. When applied as a seed dressing, BHC appears to cause no noticeable taint.

Discussion and Conclusions.

All the treatments were effective in controlling wireworms in the year of application. At the dosage level applied, good residual effects were shown by BHC broadcast, and DDT combine-drilled followed by ethylene dibromide and BHC combine-drilled. The residual effect of D-D was less marked and the BHC seed dressing showed no beneficial residual effect. While the direct effect of all the treatments may be due to a repellent or toxic action, it seems clear from the results of the wireworm sampling that the residual effects are closely associated with the effect of the treatments on the wireworm population.

When applied at 0·98 lb./acre and over, BHC tainted the potatoes grown the following year and other root crops when applied at 1·96 lb./acre and over. BHC seed treatment is economical and easily applied and there is no appreciable risk of taint of subsequent crops. Seed treatment for wireworm control has been explored to a considerable extent using BHC (Arnason & Fox, 1948; Dogger & Lilly, 1949; Hensill, 1949; Lange, Carlson & Leach, 1949; Faber, 1951; Jameson, Thomas & Tanner, 1951; Fletcher, 1952; Kulash, 1953; Kulash & Monroe, 1954). In general, good protection can be obtained in the year of application and, in some instances, reduction in wireworm population is recorded, but it appears that serious damage may be caused in subsequent years if no further treatment is given; furthermore, a seed dressing has been found inadequate in some instances where there is a very heavy infestation (Kulash, 1953; Dogger & Lilly, 1949). A number of workers have found that BHC either applied broadcast or drilled in with the seed gives good protection in the year of application and the experiments recorded have indicated that the population is reduced so that subsequent crops are not likely to suffer serious damage. However, these treatments are liable to cause taint in susceptible crops. There are now a number of records of off-flavour of crops due to various insecticides applied in the soil and this may limit their use. The conditions under which tainting of BHC can occur in England have been studied by Jameson & Tanner (1951) and Jameson & Peacock (1953), and Holmes (1951) discusses the general problem of taint by BHC. The use of refined preparations containing a high content of γ isomer appears greatly to reduce the tainting properties of this insecticide but appears not to eliminate them. The nature of the soil may influence the liability to taint by BHC (Sakurai, 1952). The experiments indicate that DDT can be used successfully to control wireworms and will reduce the population to safe limits. The data tend to confirm the results of other workers that DDT is slow to take effect (Anon., 1949; Lane & others, 1948), and it may give best results in the year of application if applied some weeks or months before planting (Ernould, 1948). The speed of action of DDT may be influenced by the type of soil (Fleming, 1950).

Although the soil fumigants gave good results in the year of application and ethylene dibromide reduced the population sufficiently to give good residual effects, the necessity for special machinery for application tends to make the fumigants compare unfavourably with the solid poisons in practice. It also seems probable that their effectiveness is more dependent on the conditions of application.

Summary.

Following crop failures due to wireworm (*Agriotes* spp.) attack on Little Hoos Field, Rothamsted, two experiments were made on the use of four chemicals to prevent wireworm attack on wheat. The chemicals used were BHC, technical DDT, ethylene dibromide and D-D.

Benzene hexachloride in the form of a dust containing 3·5 per cent. crude BHC was broadcast at the rate of 7·9 lb./acre crude BHC $\equiv$ 15·2–16·0 oz. γ isomer per acre and was combine-drilled with the seed at rates ranging from 0·98–3·92 lb./acre crude BHC $\equiv$ 1·9–8·0 oz. γ isomer per acre. It was also applied as a seed dressing at the rate of 2 oz./bushel of a dressing containing 20 per cent. technical γ isomer of BHC. DDT was drilled with the seed at 7·2 lb./acre technical DDT and ethylene dibromide and D-D were injected into the soil as soil fumigants by means of a special machine at 45·5 lb./acre and 210 lb./acre, respectively.

All these treatments gave a marked increase in yield over the control plots in the season following treatment (1947–48). The highest yields were given by the plots treated with ethylene dibromide (32·1 cwt./acre) and BHC broadcast (30·6 cwt./acre) and the lowest by the DDT treatment (20·7 cwt./acre), the corresponding untreated plots producing only 8·9 cwt./acre.

In the following year the plots were sown without further treatment, with the exception of some plots in the second experiment which were sown with seed dressed with high γ isomer BHC and one block of nine plots which was set aside for testing for possible taint with BHC treatments.

When judged on their residual effects as indicated by crop yields, plant counts and wireworm populations, BHC broadcast and combine-drilled and the plots combine-drilled with DDT gave the best results. The two soil fumigants were not so effective and there was no evidence that the BHC seed dressing had any beneficial residual effect.

Taste tests for possible tainting effects in the 1948–49 season, using lettuces, carrots, beetroot and potatoes, indicated that BHC applied to the soil at rates of 1·96 lb./acre and upwards may taint root crops, at least in the second year after treatment. The results are discussed in the light of other work on this subject.

References.

Anon. (1949). DDT for wireworm control.—Agric. Chem., **4**, no. 4, pp. 37, 39.

Arnason, A. P. & Fox, W. B. (1948). Wireworm control in the Prairie Provinces by means of BHC seed dressings.—Process. Publ. Div. Ent. Dep. Agric. Can., no. 111, 6 pp.

Arnason, A. P., Fox, W. B. & Glen, R. (1948). A preliminary test of DDT and benzene hexachloride for the control of wireworms in a Saskatchewan potato field.—Canad. Ent., **79**, pp. 174–180.

Blanka, A. (1950). Utvrdivanje majefikasnijih mjera za suzbiganje klisnjaka (Elateridae). (Determination of the most efficacious measures for the control of Elaterids).—Zaranie Slas, **2**, pp. 35–48.

Cook, W. C. (1949). Comparative studies of three soil fumigants for wireworm control.—Tech. Bull. U.S. Dep. Agric., no. 980, 22 pp.

Dogger, J. R. & Lilly, J. H. (1949). Seed treatment as a means of reducing wireworm damage to corn.—J. econ. Ent., **42**, pp. 663–665.

Ernould, L. (1948). La lutte contre les taupins.—Publ. Inst. belge Amélior. Better., **16**, pp. 299–312.

FABER, W. (1951). Versuche zur Drahtwurmbekämpfung durch Saatgutbeizung mit Hexamitteln.—PflSchBer., **6,** pp. 17–26.

FLEMING, W. E. (1950). Persistence of effect of DDT on Japanese Beetle larvae in New Jersey soils.—J. econ. Ent., **43,** pp. 87–89.

FLETCHER, F. W. (1952). Insecticides as seed treatments for the control of soil pests.—Down to Earth, **8,** pp. 16–19.

GALAKHOV, P. N. (1950). The seasonal transference of larvae of the Steppe Elater (*Agriotes gurgistanus* Fald.) in the soil and the efficiency of various measures for its control. [*In Russian.*]—Proc. Lenin. Acad. agric. Sci., **15,** pp. 31–35.

GOLIGHTLY, W. H. (1946). Modern insecticides and their use against wireworms.—Nature, Lond., **158,** p. 448.

GRAINGER, J. (1951). Soil injectors.—Res. Bull. W. Scot. Coll. Agric., no. 11, 32 pp.

HENSILL, G. S. (1949). Protection of growing plants from soil insects by use of insecticides on seeds.—Agric. Chem., **4,** no. 9, pp. 29–30.

HOLMES, E. (1951). Recent British developments in taint-free use of BHC.—Agric. Chem., **6,** no. 12, pp. 31–33, 113, 115.

INGRAM, J. W., BYNUM, E. K., CHARPENTIER, L. J. & HALEY, W. E. (1950). Chemical control of soil insects and organisms attacking sugarcane.—Sug. J., **12,** no. 10, pp. 13–14, 20.

JAMESON, H. R. & PEACOCK, F. C. (1953). Taint in potatoes grown on land treated with technical γ-benzene hexachloride or pure γ-benzene hexachloride.—J. Sci. Fd Agric., **4,** pp. 102–104.

JAMESON, H. R. & TANNER, C. C. (1951). Taint in potatoes grown on land treated with crude benzene hexachloride against wireworms.—J. Sci. Fd Agric., **2,** pp. 171–175.

JAMESON, H. R., THOMAS, F. J. D. & TANNER, C. C. (1951). The control of wireworm by gamma benzene hexachloride: the development of a seed dressing for cereals.—Ann. appl. Biol., **38,** pp. 121–134.

JAMESON, H. R., THOMAS, F. J. D. & WOODWARD, R. C. (1947). The practical control of wireworm by γ-benzene hexachloride (Gammexane): comparisons with dichlorodiphenyltrichlorethane (D.D.T.).—Ann. appl. Biol., **34,** pp. 346–356.

KING, K. M., ARNASON, A. P. & MANSON, G. F. (1948). Chemical control of wireworms in Canada.—Process. Publ. Div. Ent. Dep. Agric. Can., no. 87, 8 pp.

KULASH, W. M. (1953). Insecticidally treated seed for wireworm control.—J. econ. Ent., **46,** pp. 433–441.

KULASH, W. M. & MONROE, R. J. (1954). Laboratory tests for control of wireworms.—J. econ. Ent., **47,** pp. 341–345.

LANE, M. C., STONE, M. W., LANCHESTER, H. P., JONES, E. W. & GIBSON, K. E. (1948). Studies with DDT as a control for wireworms in irrigated lands—progress report.—U.S. Dep. Agric. Bur. Ent., E-765, 9 pp. multigraph.

LANGE JR., W. H. (1945). Ethylene dibromide and dichloropropane-dichloropropene mixture for wireworm control.—J. econ. Ent., **38,** pp. 643–645.

LANGE, W. H. (1947). New developments in soil insecticides.—Agric. Chem., **2,** no. 9, pp. 20–23, 68–69, 71.

Lange, jr., W. H., Carlson, E. C. & Leach, L. D. (1949). Seed treatments for wireworm control with particular reference to the use of lindane.—J. econ. Ent., **42,** pp. 942–955.

McClellan, W. D., Christie, J. R. & Horn, N. L. (1949). Efficacy of soil fumigants as affected by soil temperature and moisture.—Phytopathology, **39,** pp. 272–283.

Newhall, A. G. (1946). Volatile soil fumigants for plant disease control.—Soil Sci., **61,** pp. 67–82.

Pepper, B. B., Reed, J. P. & Campbell, J. C. (1949). Investigations on wireworm control with organic insecticides in New Jersey.—Amer. Potato J., **26,** pp. 315–325.

Roberts, R. (1947). Soil treatment to control *Blapstinus* wireworms.—J. econ. Ent., **40,** pp. 571–572.

Sakurai, K. (1952). On the wireworms injurious to potatoes and their control. [*In Japanese with English summary.*]—Oyō-kontyū, **8,** pp. 34–41.

Stone, M. W. (1949). Control of wireworms in California with the soil fumigants chlorinated propane-propylene and ethylene dibromide.—U.S. Dep. Agric. Bur. Ent., E-786, 21 pp.

Stone, M. W. & Foley, F. B. (1954). Field experiments with insecticides for the control of wireworms in irrigated lands.—J. econ. Ent., **46,** pp. 1075–1083.

Thomas, I. (1949). Recent research on wireworms.—Agriculture, **56,** pp. 221–228.

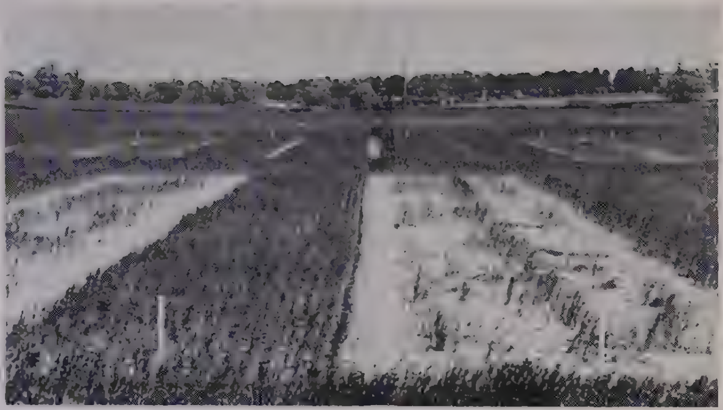


FIG. 1. DDT dust (5% technical DDT) combine drilled with the seed at 144 lb./acre≡7·2 lb. technical DDT per acre (left). Untreated (right).

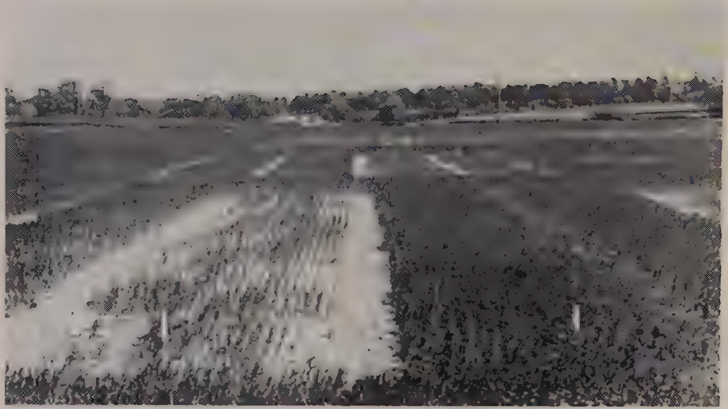


FIG. 2. Ethylene dibromide 20% v/v solution in tractor vapourising oil injected at the rate of 45·5 lb./acre ethylene dibromide (right). Untreated (left).

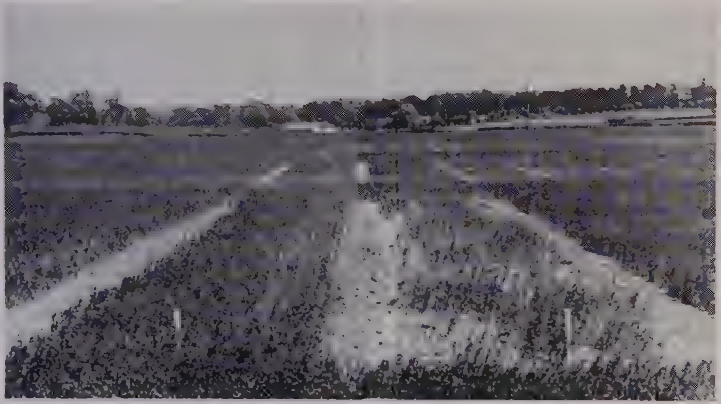


FIG. 3. DD 50% v/v solution in tractor vapourising oil injected at the rate of 210 lb./acre DD (left). Untreated (right).

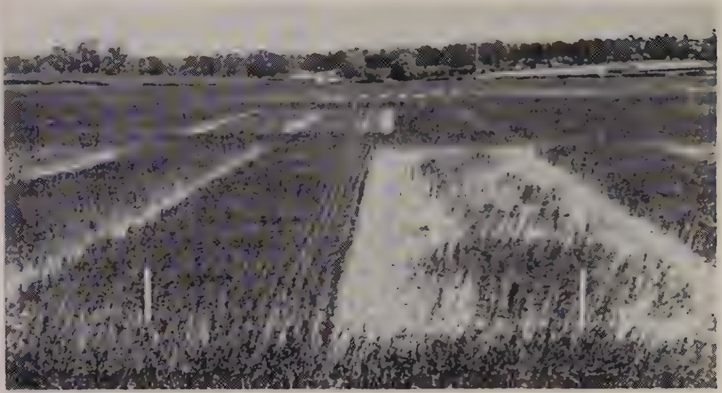


FIG. 4. BHC dust (3·5% crude BHC≡0·42–0·455% γ isomer) broadcast at 2 cwt./acre≡15·2–16·0 oz. γ isomer per acre (left). Untreated (right).

EFFECT OF VARIOUS CHEMICAL TREATMENTS FOR WIREWORM CONTROL ON THE PLANT STAND OF WHEAT.

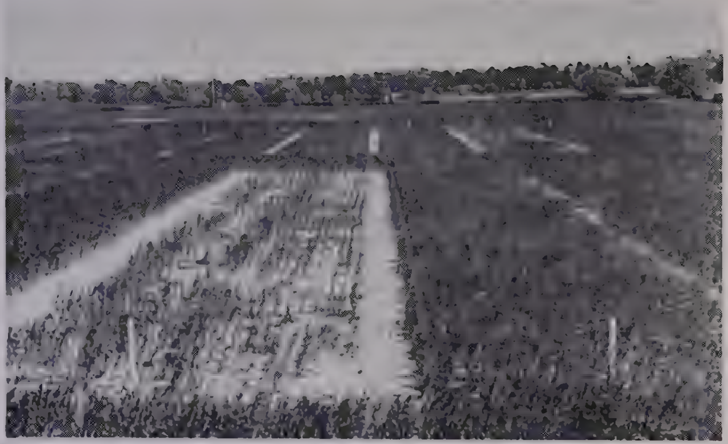


FIG. 1. BHC dust (3·5% crude BHC≡0·42–0·455% γ isomer) combine drilled with the seed at $\frac{3}{4}$ cwt./acre≡5·7–6·0 oz. γ isomer per acre (right). Untreated (left).

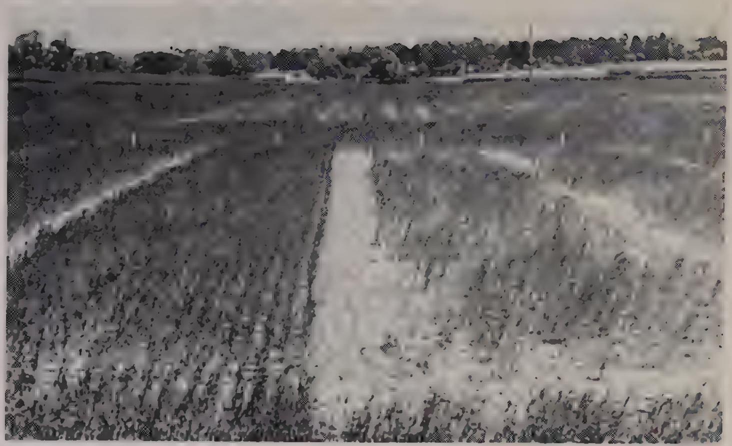


FIG. 2. Seed treated with γ BHC seed dressing at 2 oz. per bushel of a dressing containing 20% technical γ isomer (left). Untreated (right).

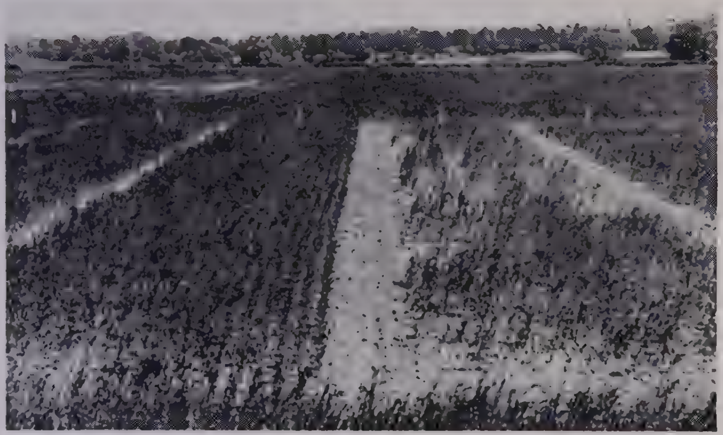


FIG. 3. BHC dust (3·5% crude BHC≡0·42–0·455% γ isomer) combine drilled with the seed at $\frac{1}{4}$ cwt./acre≡1·9–2·0 oz. γ isomer per acre (left). Untreated (right).

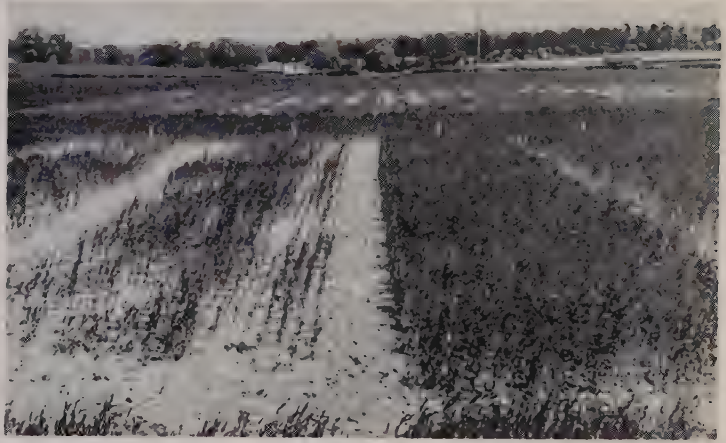


FIG. 4. BHC dust (3·5% crude BHC≡0·42–0·455% γ isomer) combine drilled with the seed at 1 cwt./acre≡7·6–8·0 oz. γ isomer per acre (right). Untreated (left).

EFFECT OF VARIOUS CHEMICAL TREATMENTS FOR WIREWORM CONTROL ON THE PLANT STAND OF WHEAT.

GENERAL INDEX.

A.

abnormalis, Aëdes (*Aëdimorphus*).
Abyssinia, *Culex zombaensis* in, **105.**
abyssinica, Evania (see *E. dimidiata*).
Acallyntrum (see *Culex*).
Acanthaspis obscura, **158, 170.**
Acanthocheilonema perstans, **438.**
Acanthoscelides obtectus, **325, 328, 331, 345, 659, 663**; dusts against, in stored pulses, **625–641.**
Acarapis woodi, infesting bees in Britain, **753–759.**
Acarus, **140.**
Achatina, **171.**
Acheta domestica, **663.**
Achroia grisella, **323, 328, 331, 345.**
Acetylcholine, effect of, on isolated cockroach heart, **205–220.**
Acyrthosiphon pisum, population studies of, in England, **369–387, 389–392**; effects of photoperiod and temperature on reproduction in, **599–624.**
Adalia bipunctata, **562, 566–572, 574, 577, 580.**
Adalia decempunctata, **562, 568, 570.**
Adelina cryptocerci, **140.**
Adenota vardoni, **59.**
adersi, Aëdes (*Diceromyia*); *Culicoides.*
adersianus, Culex (*Neoculex*).
Adrenaline, effect of, on isolated cockroach heart, **205–220.**
advena, Ahasverus.
Aëdes, **471, 472**; studies on hatching-response of eggs of, **241–254, 255–265.**
Aëdes abnormalis kabwachensis, **479.**
Aëdes adersi, **159, 163, 171, 482.**
Aëdes aegypti, **1, 2, 10, 69, 70, 84, 87, 91, 92, 94, 96, 100, 102, 103, 104, 158, 163, 165, 169–175, 177, 179, 292, 293, 296, 298, 299, 302–307, 431, 473, 498, 499, 500, 509, 555**; studies on hatching-response of eggs of, **241–254, 255–265**; bionomics of, in Kenya, **711–742.**
Aëdes aegypti queenslandensis, **84, 103, 176, 473, 738.**
Aëdes africanus, **149, 158, 163, 165, 166, 169, 173, 174, 176, 177, 178, 179, 432, 440, 496, 497, 498, 499, 500, 505, 508, 509, 514**; studies on hatching-response of eggs of, **241–254, 255.**
Aëdes albicosta, **481.**
Aëdes albocephalus, **70, 84, 88, 92, 94, 95, 100, 102, 103, 158, 160, 161, 163, 167, 168, 169, 478.**
Aëdes albopictus, **1, 3, 70, 84, 88, 92, 94, 96–102, 104, 302–306.**
Aëdes albothorax, **480.**
Aëdes amesi, **92, 93.**
Aëdes andrewsi, **3, 9.**
Aëdes apicoargenteus, **249, 431, 475, 476, 498, 499, 500, 505, 508, 514.**
Aëdes arboricolus, **85.**
Aëdes argenteopunctatus, **432, 477.**
Aëdes boneti, **92.**
Aëdes cachani (see *Uranotaenia*).
Aëdes calceatus, **159, 475, 476.**
Aëdes (*Stegomyia*) *cartroni* (see *A. pembaensis*).
Aëdes circumluteolus, **159, 163, 169, 249, 250, 432.**
Aëdes culicinus, **92.**
Aëdes cumminsi, **159, 161, 163, 169.**
Aëdes cumminsi holocinctus, **479.**
Aëdes cumminsi mediopunctatus, **161, 479.**
Aëdes dalzieli, **432.**
Aëdes dasyorrhus, **92.**
Aëdes dendrophilus, **81, 475.**
Aëdes dentatus, **159, 169.**
Aëdes domesticus, **477.**
Aëdes dufouri, **79, 80, 90, 91, 472.**
Aëdes durbanensis, **161.**
Aëdes echinus, **85.**
Aëdes edgari, **91.**
Aëdes ellinorae, **481.**
Aëdes embuensis, **159.**
Aëdes (*Stegomyia*) *fasciata* (see *A. aegypti*).
Aëdes flavimargo, **481.**
Aëdes fowleri, **104, 159, 163, 480.**
Aëdes fryeri, **70, 79, 90, 91, 103, 158, 159, 160, 161, 167, 168, 170, 171, 177, 472.**

Aëdes fulgens, **158, 159, 169, 171, 172, 472.**
Aëdes fumidus, **92, 93.**
Aëdes furcifer, **159, 161, 171, 481.**
Aëdes granti, **104.**
Aëdes haworthi, **158, 161, 171, 172, 476.**
Aëdes heischi, **158, 163, 165, 169, 171, 172, 475.**
Aëdes hirsutus, **480.**
Aëdes horrescens, **85.**
Aëdes ingrami, **158, 159, 163, 172, 249, 472.**
Aëdes kabaenensis, **93.**
Aëdes kochi, **85.**
Aëdes lamborni, **92, 479.**
Aëdes lamelliferus, **93.**
Aëdes leesoni verna, **479.**
Aëdes leptolabis, **477.**
Aëdes lineatus, **276.**
Aëdes longipalpis, **249, 250, 440, 716.**
Aëdes luteocephalus, **176.**
Aëdes marshallensis, **291, 293, 297, 299.**
Aëdes metallicus, **158, 163, 165, 171, 172, 174, 176, 432, 474, 716.**
Aëdes michaelikati, **159, 163, 169, 171, 172, 482.**
Aëdes mucidus, **471.**
Aëdes natronius, **159, 161, 163, 169.**
Aëdes ngong, **158, 161, 171, 476.**
Aëdes (*Ochlerotatus*) *nigeriensis* (see *A. fryeri*).
Aëdes nigerrimus, **471.**
Aëdes nummatus, **92.**
Aëdes ochraceus, **480.**
Aëdes papuensis, **280, 281, 282, 285, 288.**
Aëdes pembaensis, **70, 84, 88, 92, 93, 95, 96, 99, 100, 101, 103, 159, 160, 161, 167, 168, 170, 171, 177, 482.**
Aëdes polynesiensis, **292, 293, 295, 296, 298, 299.**
Aëdes pseudoscutellaris, **291, 292.**
Aëdes rhecter, **70, 84.**
Aëdes rubrithorax, **91.**
Aëdes rusticus, **249.**
Aëdes ruwenzori, **249.**
Aëdes samoanus, **292, 298, 299.**
Aëdes scatophagoides, **158, 163, 431, 471.**
Aëdes (*Stegomyia*) *scutellaris*, **1, 3, 9, 70, 277, 287, 298.**
Aëdes simpsoni, **158, 163, 165, 166, 169, 171, 172, 173, 174, 177, 179, 474.**
Aëdes soleatus, **158, 159, 169, 171, 172, 173, 476.**
Aëdes stokesi, **176.**
Aëdes subargenteus, **158, 159, 163, 165, 473.**
Aëdes tarsalis, **158, 163, 169, 478.**
Aëdes taylori, **159, 161, 171, 172, 174, 176, 481.**
Aedes teesdalei, **477.**
Aëdes tricholabis, **158, 169, 478.**
Aëdes tricholabis bwamba, **478.**
Aëdes vexans, **292, 293, 297.**
Aëdes vexans nocturnus, **297, 298, 299.**
Aëdes vigilax, **78, 79, 87, 90, 91, 95, 101, 102.**
Aëdes vigilax ludlowae, **78, 90.**
Aëdes vigilax vansomerenae, subsp.n., **70, 78–84, 87, 94, 96, 97, 98, 100, 101, 102.**
Aëdes vittatus, **2, 176, 432, 476, 496, 498, 499, 500.**
Aëdes woodi, **474.**
Aëdimorphus (see *Aëdes*).
Aëdomyia africana, **430, 468.**
Aëdomyia furfurea, **430, 468.**
aegypti, *Aëdes* (*Stegomyia*).
Aepyceros melampus (see Impala).
affine, *Mezium*.
Africa, South, *Dasynus nigromarginatus* in, **233**; *Ornithodoros zumpti* in, **747**; *Orthopodomyia* in, **104.**
africana, *Aëdomyia*; *Mansonia* (*Mansonioides*, *Taeniorhynchus*).
africanus, *Aëdes* (*Stegomyia*); *Grallatotermes*.
afrum, *Trogoderma* (see *T. granarium*).
Agama atricollis, **426, 439, 508, 511, 512, 515.**
Agamerion metallica, **139.**
Agamomermis, **171.**
Ageniaspis, **907, 908, 909, 910.**
Agral LN, **852.**
Agriotes, insecticides against, on wheat in Britain, **913–923.**
Ahasverus, **649, 652, 655, 659, 661.**
Ahasverus advena, **324, 328, 331, 345, 646, 648, 650, 651, 653, 654, 657, 660, 662.**
albiceps, *Chrysomyia*.
albicosta, *Aëdes* (*Banksinella*).
albiventris, *Culex* (*Neoculex*).
alboabdominalis, *Uranotaenia*.
albocephalus, *Aëdes* (*Aëdimorphus*).
albopictus, *Aëdes* (*Stegomyia*).
albothorax, *Aëdes* (*Banksinella*).
albus, *Staphylococcus*.
Alcephalus spp., **59, 518.** (See also Hartebeest.)
Aldabra Islands, mosquitos of, **103.**
alfierii, *Dicarnosis*.
Allacta similis, **138.**
Allodontermes morogorensis, **115, 130.**
alluaudanus, *Microtermes*.
Almond Moth (see *Ephestia cautella*).
Alphitobius, **645, 646, 653, 654, 655, 660.**
Alphitobius bifasciatus, **663.**
Alphitobius diaperinus, **324, 328, 331, 345, 346, 644, 661, 662.**
Alphitobius laevigatus (*piceus*), **324, 328, 331, 345, 346, 644, 662.**

Aluminium Pentasilicate, **633, 634, 635, 638, 639.**
amanicus, Odontotermes.
amaniensis, Odontotermes.
amanii, Coptotermes.
Amblyomma variegatum, **435.**
Amblypelta, systematic position of, **229, 235, 236, 239.**
Amblypelta bilineata, **233, 235.**
Amblypelta cocophaga, **227, 231, 233, 234, 235, 236, 239.**
Amblypelta gallegonis, **235.**
Amblypelta lutescens, **239.**
americana, Periplaneta.
amesi, Aëdes.
amicus, Basidentitermes.
Amirante Islands, mosquitos of, **102.**
Amitermes, **114, 125, 127, 134.**
Amitermes lonnbergianus, **114, 117, 118, 125.**
Amitermes unidentatus, **114, 116, 117, 118, 124.**
Ampulex assimilis, **139.**
Ampulex caniculata, **139.**
Ampulex compressa, **139.**
Ampulex compressiventris, **139.**
Ampulex fasciatus, **139.**
Ampulex ruficollis, **139.**
Ampulex siberica (see *A. compressiventris*).
Ampulex sonnerati, **139.**
Anacardium occidentale, Coreids on, **225, 233.**
Anadasynus, **236.**
anale, Sinoxylon.
analis, Callosobruchus; Corynetes.
anaphe, Tribolium.
Anarsia lineatella, **870.**
Anastatus blattidarum, **138.**
Anastatus picticornis (see *Solendenia*).
Ancistrotermes latinotus, **115, 117, 132.**
andersoni, Culex.
andrewsi, Aëdes.
Angola, pests of stored products in, **659, 661.**
angulatus, Procryptotermes.
Angulitermes truncatus, **115, 118, 129.**
Anisolabis annulipes, **664.**
Anisopteromalus calandrae, **664.**
annulioris, Culex.
annulipes, Anisolabis.
annulirostris, Culex.
Anobium punctatum, **405.**
Anopheles, **74, 90, 103.**
Anopheles coustani, **104, 158, 163, 164, 427, 464, 496, 497, 499, 500, 509, 510.**
Anopheles coustani tenebrosus, **158, 163, 465.**
Anopheles coustani ziemanni, **427, 464, 497.**
Anopheles farauti, **275, 276, 277, 283, 299.**
Anopheles funestus, **158, 163, 164, 425, 428, 437–444, 465, 495–515.**
Anopheles funestus confusus, **428.**
Anopheles gambiae, **69, 97, 103, 104, 158, 163, 164, 428, 437–444, 466, 495–515.**
Anopheles hyrcanus, **458.**
Anopheles implexus, **465.**
Anopheles keniensis, **466.**
Anopheles leesoni, **158, 163.**
Anopheles longipalpis, **428, 439, 507, 510, 514.**
Anopheles lungae, **281.**
Anopheles maculatus, **302–306.**
Anopheles maculipalpis, **429, 439, 466, 496, 510.**
Anopheles maculipennis atroparvus, **302, 303, 304, 306.**
Anopheles marshalli, **466.**
Anopheles multicolor, **457, 458.**
Anopheles nili, **465.**
Anopheles paludis, **465.**
Anopheles pharoensis, **158, 163, 429, 440, 466, 496, 499, 500, 501, 505, 506, 514.**
Anopheles punctulatus, **275, 280, 282, 283, 285, 286.**
Anopheles punctulatus moluccensis (see *A. farauti*).
Anopheles quadrimaculatus, **302, 303, 304.**
Anopheles rhodesiensis, **158, 163, 429, 440, 466, 508, 509, 510, 511, 513, 515.**
Anopheles rivulorum, **429, 465, 500.**
Anopheles rivulorum garnhamellus, **429.**
Anopheles rufipes, **429, 439, 496, 510.**
Anopheles sacharovi, **448, 449, 450, 451, 453, 458.**
Anopheles sergentii, bionomics of, in Israel, **445–462.**
Anopheles solomonis, **275, 278, 281, 282, 284, 285, 286.**
Anopheles squamosus, **430, 466, 496.**
Anopheles subpictus, **1.**
Anopheles superpictus, **281, 448, 449, 450, 452, 453, 456, 457, 458, 459.**
Anopheles tessellatus, **1.**
Anopheles wellcomei, **430, 496.**
Anoplotermes, **115, 118, 119, 120, 121, 126, 127, 129.**
Anoplotermes kilimandjaricus, **115, 126.**
Anoplotermes lateralis, **115, 126.**
Antbear, **536.**
Antelope, Roan, **518, 532, 533, 534, 535, 536.**
antennatus, Culex.
Anthicus floralis, **663, 665.**
Anthrenocerus australis, **324, 328, 331, 345, 347, 348.**

Anthrenus verbasci, **324, 328, 332, 345, 346.**
Anthrenus vorax, **324, 328, 332, 343, 345, 347, 348, 661, 663.**
antiqua, Delia.
Apanteles bordagei, **904.**
Aphanogmus fumipennis, **37.**
Aphanus sordidus, **663, 665.**
Aphis fabae, Coccinellids associated with, on beans in Britain, **561–587.**
apicoargenteus, Aëdes (*Stegomyia*).
apis, Nosema.
Apolygus (see *Lygus*).
appendiculata, Leidynema.
appendiculatus, Rhipicephalus.
appendigaster, Evania.
Apple, *Thomasiniana* spp. on, **27–32, 34, 36.**
Arabia, parasite of cockroaches in, **142.**
arachidis, Prolabia.
Araecerus fasciculatus, **323, 325, 328, 345, 645, 646, 648–651, 655, 656, 659–662.**
arboricolis, Orthopodomyia.
arboricolus, Aëdes (*Stegomyia*).
arenicolous, Ornithodoros.
argenteopunctatus, Aëdes (*Aëdimorphus*); *Culex.*
argyrurus, Paraëdes.
Armigeres, **762.**
Armigeres obturbans, **1.**
ascidiicola, Uranotaenia.
assimilis, Ampulex.
Atelerix pruneri, **426, 439, 508, 511, 512.**
ater, Dermestes.
Atilax paludinosus mordax (see Mongoose, Marsh).
atroparvus, Anopheles maculipennis.
Atropine, effect of, on isolated cockroach heart, **205–220.**
Attagenus gloriosae, **661, 663, 665.**
Attagenus megatoma (*piceus*), **324, 328, 332, 345, 661, 663.**
Attagenus pellio, **324, 328, 332, 345, 346, 401, 405, 408, 410–414, 416.**
Aulacosternum, distinct from *Dasynus*, **236.**
aurantapex, Culex.
auricularia, Forficula.
austeni, Glossina.
Austenina (see *Glossina*).
australasiae, Periplaneta; Protrellina; Tetrastichus.
australe, Ellipsidion.
Australia, *Ceroplastes* spp. in, **267**; *Ornithodoros capensis* in, **747.**
australis, Anthrenocerus.
Azizus, **158, 163.**

B.

Baboon, **59, 518, 532, 534, 536**; tick on, **170.**
Bacon Beetle (see *Dermestes lardarius*).
badius, Odontotermes.
Balantidium ovatum, **140.**
Balantidium praenucleatum, **140.**
balfouri, Uranotaenia.
Banana, *Amblypelta lutescens* on, **239.**
bancrofti, Wuchereria.
Banksinella (see *Aëdes*).
Barley, Stored, pests in, **402.**
Basidentitermes amicus, **115, 128.**
Bassas da India Islands, mosquitos of, **103.**
Bats, **427, 439, 508, 511, 512, 513, 536.**
Bean Aphid, Black (see *Aphis fabae*).
Bean Beetle (see *Acanthoscelides obtectus*).
Bean Seed Fly (see *Delia cilicrura* and *D. trichodactyla*).
Beans, Broad or Field (see *Vicia faba*).
Beans, Stored, dusts against Bruchids in, **625–641.**
Bees, Honey, acarine and *Nosema* diseases of, in Britain, **753–759.**
Beet, tainted by BHC, **919–920.**
bellicosi, Promirotermes.
bellicosus, Macrotermes.
Bengalia floccosa, preying on termites and ants in Tanganyika, **134.**
bergrothi, Lathridius.
bettonianus, Trinervitermes.
BHC, **137, 301–309, 402, 548, 549, 550, 625–641, 681, 913–923**; toxicity and interaction of stereo-isomers of, in cockroaches, **837–843.**
bibliophagum, Dorcatoma.
bifasciatus, Alphitobius.
bifoveolatus, Dinoderus.
bilineata, Amblypelta; Uranotaenia.
bipunctata, Adalia.
Biscuit Beetle (see *Stegobium paniceum*).
Bis(dimethylamino)fluorophosphine Oxide (see Dimefox).
Bisdimethylaminophosphonous Anhydride (see Schradan).
bisselliella, Tineola.
bitaeniorhynchus, Culex.
Bitoma, **663.**
Blackberry, *Thomasiniana* spp. on, **27–36.**
Blackberry Cane Midge (see *Thomasiniana fruticosi*).
Blackthorn, *Thomasiniana oculiperda* ovipositing on, **28, 29, 30.**
Blatta orientalis, **205, 323, 328, 332, 345, 347, 663**; parasites and predators of, **137–147.**

blattae, Blatticola; Endamoeba; Endolimax; Retortamonas.
blattarum, Gregarina; Lophomonas; Plagiostoma (*Bursaria*); *Symbius* (see *Rhipidius pectinicornis*).
Blattella germanica, **663**; parasites and predators of, **137–147.**
Blatticola blattae, **140.**
blattidarum, Anastatus.
blattiphagus, Solendenia (see *Anastatus blattidarum*).
Blattotetrastichus hagenowii (see *Tetrastichus*).
boneti, Aëdes.
boranicus, Odontotermes.
borboricus, Eulophus.
bordagei, Apanteles.
Brachygaster minutus, **138.**
brachygnathus, Microcerotermes.
Brachypeplus, **663.**
Bracon hebetor, **664.**
brassicae, Erioischia.
brevicauda, Ceroplastes.
brevipalpis, Culex (*Neoculex*); *Glossina* (*Austenina*); *Toxorhynchites* (*Megarhinus*).
brevirostris, Uranotaenia.
brevistylus, Dacus (see *D. ciliatus*).
Britain, *Acyrthosiphon pisum* in, **369–387, 389–392**; studies on Anthomyiid flies in, **11–19, 21–26**; diseases of bees in, **753–759**; Coccinellids associated with *Aphis fabae* in, **561–587**; cockroaches in, **137**; *Pristiphora glauca* on larch in, **749–752**; identity and bionomics of Tarnished Plant Bug in, **846**; *Thomasiniana* spp. in, **27–38**; wireworms in, **913–923**; pests of stored products in, **311–355, 399–417, 643–668, 773, 781, 813–835.**
Broad Beans (see *Vicia faba*).
browni, Tetrastichus (see *T. hagenowii*); *Uranotaenia.*
brumpti, Uranotaenia.
brunneus, Heterobostrychus; Lyctus.
bucculentus, Dasynus.
Bucorvus cafer (see Hornbill, Ground).
Bud Borer, Red (see *Thomasiniana oculiperda*).
Buffalo, **59, 518, 532, 533, 534, 536.**
Bufo regularis, **426.**
Bulbul, **509.**
bulhoesi, Thelastoma.
Bullfrog, African (see *Rana occipitalis*).
buqueti, Thaneroclerus.
Bursaria blattarum (see *Plagiostoma*).
Bushbuck, **59, 518, 532, 533, 534, 536, 537.**
Bushpig, **59, 518, 532, 533, 534, 536.**
bwamba, Aëdes (*Aëdimorphus*) *tricholabis.*

C.

Cabbage, persistence of DDT deposits on wax and leaves of, **39–56, 849–868.**
Cabbage Root Fly (see *Erioischia brassicae*).
Cabinet Beetle, Larger (see *Trogoderma versicolor*).
Cacao, pests and virus diseases of, in Gold Coast, **669–710**; new Coreid on, in Zanzibar, **224.**
Cacao, Stored, pests of, **643–668.**
Cacao Moth (see *Ephestia elutella*).
Cacao Weevil (see *Araecerus fasciculatus*).
cachani, Uranotaenia (*Aëdes, Skusea*).
Cadelle (see *Tenebroides mauritanicus*).
caffeina, Leucoptera.
Calandra granaria, **325, 328, 333, 334, 345, 346, 399–417, 662.**
Calandra oryzae, **322, 323, 325, 328, 334, 339, 345, 346, 347, 400, 402, 403, 405, 413, 415, 416, 662, 663, 805.**
calandrae, Anisopteromalus.
calceatus, Aëdes (*Stegomyia*).
calcitrans, Stomoxys.
Callosobruchus analis, **325, 328, 335, 345.**
Callosobruchus chinensis, **325, 328, 335, 345, 659, 663**; dusts against, in stored pulses, **625–641.**
Callosobruchus maculatus, **661, 663.**
Calomel (see Mercurous Chloride).
Cameroons, French, *Pseudotheraptus devastans* in, **227.**
campestris, Lyctocoris.
candidipes, Uranotaenia.
canescens, Nemeritis.
caniculata, Ampulex (*Rhinopsis*).
capensis, Hippobosca; Ornithodoros.
capitis, Pediculus humanus.
capitata, Ceratitis.
Carbon Tetrachloride, **551, 552, 553.**
Carcinops quattuordecimstriata, **663.**
carmelita, Theraptus (*Pendulinus*).
Carnauba Wax, **42.**
carnivorus, Dermestes.
Carpet Beetle, Australian (see *Anthrenocerus australis*).
Carpet Beetle, Black (see *Attagenus megatoma*).
Carpet Beetle, Furniture (see *Anthrenus vorax*).
Carpet Beetle, Varied (see *Anthrenus verbasci*).
Carpet Moth (see *Trichophaga tapetzella*).
Carpocapsa (see *Cydia*).
Carpophilus, **645, 646, 648–656, 659, 660, 661.**

Carpophilus dimidiatus, **324, 328, 335, 345, 644, 662.**
Carpophilus hemipterus, **324, 328, 335, 345, 346, 644, 662.**
Carpophilus ligneus, **324, 328, 335, 345, 346, 644, 663.**
Carpophilus maculatus, **644, 663.**
Carpophilus obsoletus, **644, 662.**
Carrot, tainted by BHC, **919–920.**
cartroni, *Aëdes* (*Stegomyia*) (see *A. pembaensis*).
Caryedon fuscus, **325, 328, 335, 345, 645, 646, 653, 654, 655, 660, 662, 664.**
Cassava, arthropod population of the soil under, in Uganda, **540, 542.**
castaneum, *Tribolium*.
Cathartus quadricollis, **663.**
catillus, *Piestopleura*.
Caulophilus latinasus, **325, 328, 335, 345.**
cautella, *Ephestia*.
cellaris, *Cryptophagus*.
cephalonica, *Corcyra*.
Ceratitis capitata, fumigation against, in *Citrus* fruits in Israel, **803–811.**
Cercopithecus spp. (see Monkeys).
cerealella, *Sitotroga*.
Cereals, Stored, pests of, **399–417, 773–780, 781–796.**
ceriferus, *Ceroplastes*.
Cerococcus, **271.**
Ceroplastes brevicauda, **267, 268, 269.**
Ceroplastes ceriferus, **267.**
Ceroplastes destructor, host-plants and distribution of, **267, 269, 273.**
Ceroplastes destructor brevicauda (see *C. brevicauda*).
Ceroplastes luteolus, sp.n., **268.**
Ceylon, *Ornithodoros savignyi* in, **748.**
Chagos Archipelago, mosquitos of, **102.**
chalybii, *Melittobia*.
Chameleon dilepsis, **426.**
Cheiloneurus viridiscutum, **139.**
Cherry, *Thomasiniana oculiperda* ovipositing on, **29.**
Chimaeropsylla haddowi, **159, 170.**
chinensis, *Callosobruchus*.
chloropyga, *Chrysomyia*.
Chrysanthemum, *Lygus rugulipennis* on, **845.**
chrysogaster, *Eretmapodites*.
Chrysomyia albiceps, **111, 434.**
Chrysomyia chloropyga, **111.**
Chrysomyia marginalis, **111.**
Chrysomyia putoria, **111, 434.**
Chrysops distinctipennis, **434.**
Chrysops longicornis, **159.**
chrysosoma, *Mansonia* (*Coquillettidia*, *Taeniorhynchus*).
Ciconia ciconia, **59.**
Cigarette Beetle (see *Lasioderma serricorne*).
ciliatus, *Dacus*.
cilicrura, *Delia*.
Cimex hemipterus, **434.**
Cineraria, persistence of DDT deposits on leaves of, **849–868.**
cinereus, *Culex* (*Culiciomyia*).
cinerellus, *Culex* (*Culiciomyia*).
circumluteolus, *Aëdes* (*Banksinella*).
Citrus, *Dasynus nigromarginatus* on, **233**; fumigation of fruits of, against *Ceratitis capitata*, **803–811.**
Citrus maxima, new Coccid on, **269.**
civinskii, *Uranotaenia*.
Clinodiplosis oleisuga (see *Thomasiniana*).
Clothes Moth (see *Tineola bisselliella*).
Coarctotermes coarctatus, **115, 133.**
Cobra, Black-necked (see *Naja nigricollis*).
Cobus (see Waterbuck).
Coccinella septempunctata, **371, 562, 567–572, 574, 580.**
Coccinella undecimpunctata, **562, 567, 580.**
coccinellae, *Perilitus*.
coccocinctus, *Dasynus*.
Coccotrypes, **663.**
cochleariae, *Phaedon*.
Cockroaches, parasites and predators of, **137–147.** (See also *Blatta* and *Periplaneta*.)
Cocoa (see Cacao).
Coconut, Coreids and early nutfall of, **221, 222, 225, 235, 239.**
cocophaga, *Amblypelta*.
Codling Moth (see *Cydia pomonella*).
Coelosporidium periplanetae, **140.**
coeruleocephala, *Tripteroides*.
Coetivy Island, mosquitos of, **103.**
Coffee (*Coffea* spp.), pests of, in East Africa, **267–273, 899–912.**
coffeella, *Leucoptera*.
coffeicola, *Pleurotropis*.
Cold-hardiness, in insects, **311–355, 813–835.**
Colobus (see Monkeys).
columbariella, *Tinea*.
combesi, *Uranotaenia*.
Comoro Islands, mosquitos of, **103.**
Comperia falsicornis, **138.**
compressa, *Ampulex*.
compressiventris, *Ampulex*.
conchobius, *Eretmapodites silvestris*.
concinnulus, *Monanus*.
condei, *Eretmapodites* (see *E. quinquevittatus*).
confusum, *Tribolium*.
confusus, *Anopheles funestus*.

Congo, Belgian, *Ornithodoros savignyi* doubtfully occurring in, **748**; pests of stored products in, **661**, **662**.
coniceps, *Ornithodoros*.
Coninomus constrictus, **663**.
consimilis, *Culex annulioris*.
constrictus, *Coninomus*.
Copra Beetle (see *Necrobia rufipes*).
Coptotermes amanii, **114**, **116**, **118**, **124**.
Coquillettidia (see *Mansonia*).
Corcyra cephalonica, **323**, **643–668**.
Corethrella, **281**, **288**.
Corn Moth (see *Tinea granella*).
Corn Sap Beetle (see *Carpophilus dimidiatus*).
cornutus, *Gnathocerus*.
Corticaria fulva, **405**.
Corynetes analis, **663**.
Cosmoledo Islands, mosquitos of, **103**.
Cotton, *Dysdercus* spp. on, in Uganda, **743**.
coursi, *Culex*.
coustani, *Anopheles*.
Cowpea Beetle (see *Callosobruchus chinensis*).
CR. 409 (see Dimefox).
Crabs, **99**, **170**, **171**, **295**.
crataegi, *Thomasiniana*.
Crataegus oxyacantha (see Hawthorn).
Crematogaster, **671**, **675**, **681**.
Crenetermes, **118**, **127**.
Crenetermes umbraticola, **115**, **126**.
Cricetomys gambianus osgoodi, flea on, **170**.
crinita, *Xenopsylla*.
Crocodilus niloticus, **426**.
crudelis, *Haematopota*.
cryptocerci, *Adelina*.
Cryptophagus, **401**, **402**, **410**, **662**.
Cryptophagus cellaris, **405**, **663**.
Cryptophagus distinguendus, **405**.
Cryptophagus obsoletus, **405**.
Cryptophagus pilosus, **405**.
Cryptophagus saginatus, **405**.
Cryptotermes havilandi, **114**, **116**, **123**.
Ctenocephalides felis felis, **159**, **170**.
Cubitermes, **125**, **126**, **132**, **134**.
Cubitermes glebae, **115**, **117**, **118**, **120**, **127**.
Cubitermes umbratus, **115**, **117**, **118**, **120**, **126**, **127**.
Culex, **163**, **169**, **171**; corrections to Hopkins' key to larvae of, **105**.
Culex adersianus, **485**.
Culex albiventris, **159**, **161**, **485**.
Culex andersoni, **93**.
Culex annulioris, **159**, **163**, **433**, **439**, **440**, **487**, **496**, **497**, **499**, **500**, **505–515**.
Culex annulioris consimilis, **433**.
Culex annulirostris, **283**, **285**, **292**, **293**, **296**, **297**, **298**, **299**; abnormal larvae of, in Tonga, **185–188**.
Culex antennatus, **70**, **159**, **163**, **166**, **433**, **440**, **489**, **496**, **497**, **500**, **501**, **505**, **509**, **514**.
Culex argenteopunctatus kingi, **433**, **488**.
Culex aurantapex, **159**, **163**.
Culex bitaeniorhynchus, **486**.
Culex brevipalpis, **4**, **93**.
Culex cinerellus, **486**.
Culex cinereus, **485**.
Culex coursi, **93**.
Culex decens, **93**, **159**, **171**, **434**, **440**, **489**, **490**, **509**, **716**.
Culex demeilloni, **93**.
Culex duttoni, **434**, **440**, **488**.
Culex ethiopicus, **486**, **487**.
Culex femineus, **276**.
Culex fragilis, **285**.
Culex fraudatrix, **278**, **285**.
Culex furlongi, **486**.
Culex gelidus, **302**, **303**, **304**, **306**, **307**.
Culex grahami, **491**.
Culex guiarti, **490**.
Culex halifaxii, **283**, **285**.
Culex hancocki, **86**, **93**, **94**.
Culex hayashii, **93**.
Culex horridus, **93**, **159**, **172**, **485**.
Culex inconspicuosus, **486**.
Culex infantulus, **1**, **5**, **10**.
Culex insignis, **104**, **484**.
Culex invidiosus, **489**.
Culex kingianus, **105**.
Culex malayi, **1**.
Culex mauritanicus, **93**.
Culex minutissimus, **1**, **3**, **5**.
Culex mirificus, **161**.
Culex moucheti, **90**, **491**.
Culex musarum, **86**, **93**, **94**.
Culex nebulosus, **159**, **161**, **172**, **173**, **176**, **485**, **716**.
Culex nebulosus pseudocinereus, **161**.
Culex ornatothoracis, **93**, **490**.
Culex pallidothorax, **285**.
Culex papuensis, **283**, **285**, **286**, **288**.
Culex parainfantulus (see *C. infantulus*).
Culex perexiguus (see *C. univittatus*).
Culex perfuscus, **490**.
Culex perkinsi, **280**, **285**, **286**.
Culex pipiens fatigans, **1**, **70**, **86**, **89**, **93**, **94**, **96**, **97**, **98**, **100**, **101**, **102**, **103**, **104**, **159**, **161**, **163**, **166**, **167**, **168**, **169**, **176**, **292**, **293**, **296**, **301–309**, **489**, **716**.
Culex pipiens molestus, **302**, **303**, **304**, **306**, **307**.
Culex pipiens pipiens, **86**, **159**, **161**, **163**, **166**, **167**.
Culex poicilipes, **104**, **159**, **161**, **163**, **177**, **432**, **486**, **508**, **509**, **510**.

Culex pullus, **283, 285.**
Culex quasiguiarti, **159, 169, 489.**
Culex robici, **93.**
Culex scotti, **69, 70, 86, 89, 93, 94, 95, 96, 100.**
Culex seldeslachtsi, **105.**
Culex semibrunneus, **486.**
Culex simpsoni, **70, 85, 86, 89, 93, 94, 96, 97, 98, 100, 101, 102, 105, 488.**
Culex sinaiticus, **93, 105.**
Culex sitiens, **1, 7, 103, 159, 167, 168, 296, 298, 487.**
Culex spathifurca, **1, 10.**
Culex squamosus, **278, 283, 285.**
Culex stellatus, **70, 75, 77, 85, 88, 93, 94, 95, 98, 100.**
Culex stylifurcatus (see *C. spathifurca*).
Culex sumatranus, **93.**
Culex thalassius, **176.**
Culex theileri, **103, 105.**
Culex tigripes, **104, 159, 169, 432, 484, 508.**
Culex trifoliatus, **490.**
Culex tritaeniorhynchus, **1, 6, 7, 104, 487.**
Culex univittatus, **105, 159, 163, 167, 168, 169, 177, 433, 439, 440, 488, 496, 499, 505–515.**
Culex univittatus neavei, **433, 440, 488, 509.**
Culex vishnui, **1.**
Culex weschei, **491.**
Culex weschei gediensis, **490, 491.**
Culex wigglesworthi, **484.**
Culex zombaensis, **105, 159, 161, 163, 166.**
Culicelsa (see *Aëdes*).
culiciformis, Empicoris.
culicinus, Aëdes (*Aëdimorphus*).
Culiciomyia (see *Culex*).
Culicoides adersi, **159, 170.**
culturarum, Odontotermes.
cumminsi, Aëdes (*Aëdimorphus*).
Cutilia soror, **138.**
Cydia (*Grapholitha*) *molesta*, in U.S.A., **870–871**; development and fecundity of, under controlled conditions, **869–898.**
Cydia nigricana, **371.**
Cydia (*Carpocapsa*) *pomonella*, **870, 874, 878, 881, 888, 894, 895.**
cylindricum, Pentarthrum.

D.

Dacus ciliatus (*brevistylus*), **111.**
dalzieli, Aëdes (*Aëdimorphus*).
Dasynus, characters of, **229, 234.**
Dasynus bucculentus, **235.**
Dasynus coccocinctus, **227, 231, 233, 234, 235, 236.**
Dasynus (*Theraptus*) *distanti*, **232, 233.**
Dasynus (*Theraptus*) *nigromarginatus*, **227, 232, 233, 236.**
dasyorrhus, Aëdes.
D-D, **914–917.**
DDT, **137, 301–309, 371, 451–455, 459, 460, 634, 636–639, 914–917**; effect of, on isolated cockroach heart, **205–220**; persistence of deposits of, on foliage, **39–56, 849–868**; sorption of, by mud blocks, **547–559.**
Decco, **807, 808, 809, 810.**
decempunctata, Adalia.
decens, Culex.
decipiens, Loboptera.
delanoei, Ornithodoros.
Delia antiqua, bionomics of, in Britain, **11–14, 21–26.**
Delia cilicrura, bionomics of, in Britain, **16–17, 21–26.**
Delia trichodactyla, **16–17.**
demeilloni, Culex.
dendrophilus, Aëdes (*Stegomyia*).
dentatus, Aëdes (*Aëdimorphus*).
depressa, Lyphia.
Dermestes, **140, 645, 646, 660.**
Dermestes ater, **644, 661, 662.**
Dermestes carnivorus, **644, 661, 663.**
Dermestes frischii, **323, 328, 335, 345, 644, 661, 663.**
Dermestes lardarius, **324, 328, 335, 345, 346, 644, 663.**
Dermestes maculatus, **323, 328, 336, 345, 346, 644, 661, 662.**
Dermestes vulpinus (see *D. maculatus*).
destructor, Ceroplastes; Tribolium.
devastans, Pseudotheraptus (*Pendulinus, Theraptus*).
diaperinus, Alphitobius.
Diatomite, **627–639.**
Dicarnosis alfierii, **139.**
Diceromyia (see *Aëdes*).
Diceros bicornis (see Rhinoceros).
Dichloropropane, and dichloropropene, mixture of (see D-D).
Dieldrin, **301–309, 555.**
diesingi, Hammerschmidtiella.
Diethyl p-Nitrophenyl Phosphate (see Paraoxon).
Diethyl p-Nitrophenyl Thiophosphate (see Parathion).
Dikdik, **518.**
Dimefox, **669–710.**
dimidiata, Evania.
dimidiatus, Carpophilus.
Dinoderus bifoveolatus, **663.**
Dinoderus minutus, **663.**
Diocalandra impressicollis, **663.**

Diplocystis schneideri, **140.**
distanti, *Dasynus* (*Theraptus*).
distinctipennis, *Chrysops*.
distinguendus, *Cryptophagus*.
Dock, persistence of DDT deposits on leaves of, **849–868.**
Dog, *Hippobosca capensis* on, **170.**
domestica, *Acheta; Musca; Thermobia*.
domesticus, *Aëdes* (*Aëdimorphus*); *Spiniger*.
dominica, *Rhizopertha*.
Dorcatoma bibliophagum, **324, 328, 336, 345.**
Dormouse, Forest (see *Graphiurus murinus*).
Dorylaea rhombifolia (see *Neostylopyga*).
Dried-currant Moth (see *Ephestia cautella*).
Dried-fruit Beetle (see *Carpophilus hemipterus*).
Drugs, physiological action of, on isolated cockroach heart, **205–220.**
dufouri, *Aëdes* (*Ochlerotatus*).
Duiker, **59, 518, 532–536.**
Duiker, Blue, **59.**
dumicola, *Pericapritermes*.
Dunnius (see *Aëdes*).
durbanensis, *Aëdes; Kalotermes*.
Dusts, Inert, against pests of stored pulses, **631–635, 639.**
duttoni, *Culex*.
Dysdercus, rearing of, **743–746.**

E.

Echidnophaga, **435.**
echinus, *Aëdes* (*Finlaya*).
Ectobius lapponicus, **138.**
Ectobius (*Ectobia*) *lividus*, **139.**
edentatus, *Microcerotermes*.
edgari, *Aëdes*.
Egypt, *Ornithodoros* spp. in, **747**; identity of common *Trogoderma* in, **773–775.**
Eland, **59, 533.**
Elasmus leucopterae, **908.**
Elephant, **59, 518, 532, 533, 534, 536.**
Ellice Islands, mosquitos of, **291–300.**
ellinorae, *Aëdes* (*Banksinella*).
Ellipsidion australe, **139.**
Ellipsidion pellucidum, **138, 139.**
embuensis, *Aëdes*.
Empicoris culiciformis, **404.**
Endamoeba blattae, **140.**
Endamoeba thomsoni, **140.**
Endolimax blattae, **140.**
Endrosis sarcitrella, **400, 401, 405, 663.**
Enicmus minutus, **401, 405, 663.**
Entedon hagenowii (see *Tetrastichus*).
Ephestia, **649, 655.**
Ephestia cautella, **323, 328, 336, 339, 345, 402, 405, 643–668**; experiments on winter survival of, in Britain, **813–835.**
Ephestia elutella, **323, 328, 336, 345, 400–404, 408, 410, 412, 413, 414, 643, 644, 663, 831.**
Ephestia kuehniella, **323, 328, 336, 345, 348, 663, 831.**
Epomophorus wahlbergi, **426, 439, 508, 511, 512.**
Equus burchelli (see Zebra).
erebus, *Platymeris*.
Eretmapodites, biting-habits of, in Uganda, **761–772.**
Eretmapodites chrysogaster, **85, 159, 161, 163, 169, 171, 172, 173, 716, 761–772.**
Eretmapodites condei (see *E. quinquevittatus*).
Eretmapodites ferox, **761, 762, 764, 767, 768, 769, 770.**
Eretmapodites gilletti, **761, 763.**
Eretmapodites grahami, **761, 763.**
Eretmapodites haddowi, **761, 763.**
Eretmapodites harperi, **761, 763.**
Eretmapodites inornatus, **483, 761, 764, 769, 770.**
Eretmapodites intermedius, **161, 761, 763.**
Eretmapodites leucopus productus, **761, 762, 769.**
Eretmapodites mahaffyi, **761, 763.**
Eretmapodites oedipodius, **159, 171.**
Eretmapodites oedipodius parvipluma, **484, 761, 762, 764, 766, 767, 768, 770.**
Eretmapodites penicillatus, **761.**
Eretmapodites plioleuca, **103.**
Eretmapodites quinquevittatus, **103, 159, 171, 483, 716, 761.**
Eretmapodites semisimplicipes, **761, 763.**
Eretmapodites silvestris conchobius, **159, 169, 171, 483.**
Eretmapodites subsimplicipes, **482.**
Eretmapodites tonsus, **761.**
Ergotamine, effect of, on isolated cockroach heart, **205–220.**
Erioischia brassicae, **14–15.**
Erioischia floralis, **15–16.**
Erithacus rubecula (see Robin).
erratica, *Lecaniodiaspis*.
erraticus, *Ornithodoros*.
Eserine, effect of, on isolated cockroach heart, **205–220.**
Ethanol, **851.**
ethiopicus, *Culex*.
Ethylene Dibromide, **803–811, 914–917.**
Etorleptiomyia (see *Ficalbia*).

Euchilotermes, **115, 118, 127.**
Eulophus borboricus, **908, 909.**
Evania abyssinica (see *E. dimidiata*).
Evania appendigaster, **138.**
Evania dimidiata, **138.**
Evania impressa, **138.**
Evania laevigata, **138.**
Evania punctata, **138.**
Evania sericea, **138.**
Evania subspinosa, **138.**
evansi, Microlophium.
Exolygus (see *Lygus*).

F.

fabae, Aphis.
falciparum, Plasmodium.
falsicornis, Comperia.
farauti, Anopheles (*Myzomyia*).
farinae, Tyroglyphus.
farinalis, Pyralis.
fasciata, Aëdes (*Stegomyia*) (see *A. aegypti*).
fasciatus, Ampulex.
fasciculatus, Araecerus.
fatigans, Culex pipiens.
felis, Ctenocephalides felis.
femineus, Culex (*Mochthogenes*).
fenestralis, Scenopinus.
ferox, Eretmapodites.
ferrugineus, Laemophloeus.
Ficalbia, **69.**
Ficalbia hispida, **469.**
Ficalbia lacustris, **430, 469.**
Ficalbia mediolineata, **470.**
Ficalbia mimomyiaformis, **469.**
Ficalbia pallida, **469.**
Ficalbia plumosa, **469.**
Ficalbia splendens, **430, 469.**
Ficalbia uniformis, **430, 470.**
Field Beans (see *Vicia faba*).
Filaria rhytipleurites, **140.**
Filariasis (see *Wuchereria*).
filum, Leurostenus.
Finlaya (see *Aëdes*).
flavimargo, Aëdes (*Banksinella*).
flavipes, Xylocoris.
floccosa, Bengalia.
floralis, Anthicus; Erioischia.
floridanus, Tetrastichus (see *T. hagenowii*).
Flour Beetle, Broad-horned (see *Gnathocerus cornutus*).
Flour Beetle, Confused (see *Tribolium confusum*).
Flour Beetle, Dark (see *Tribolium destructor*).
Flour Beetle, Depressed (see *Palorus subdepressus*).
Flour Beetle, Long-headed (see *Latheticus oryzae*).
Flour Beetle, Rust-red (see *Tribolium castaneum*).
Flour Beetle, Small-eyed (see *Palorus ratzeburgi*).
Flour Moth, Mediterranean (see *Ephestia kuehniella*).
foleyi, Ornithodoros.
Forficula auricularia, **664.**
Formosa, *Aëdes vigilax* in, **87, 90.**
fowleri, Aëdes (*Aëdimorphus*).
fragilis, Culex.
fraseri, Uranotaenia bilineata.
fraternus, Tabanus.
fraudatrix, Culex (*Lophoceraomyia*).
frischii, Dermestes.
Fruit-bat, Epauletted (see *Epomophorus wahlbergi*).
Fruit-fly, Mediterranean (see *Ceratitis capitata*).
Fruit Moth, Oriental (see *Cydia molesta*).
fruticosi, Thomasiniana.
fryeri, Aëdes (*Culicelsa, Ochlerotatus*).
fulgens, Aëdes (*Finlaya*).
fulva, Corticaria.
fulvipes, Orphinus.
fumidus, Aëdes.
fumipennis, Aphanogmus.
funestus, Anopheles (*Myzomyia*).
Fungus Beetle, Black (see *Alphitobius laevigatus*).
fur, Ptinus.
Fur Beetle (see *Attagenus pellio*).
furcifer, Aëdes (*Diceromyia*).
furfurea, Aëdomyia.
furlongi, Culex (*Culiciomyia*).
fusca, Uranotaenia.
fuscopennatus, Mansonia (*Coquillettidia, Taeniorhynchus*).
fuscus, Caryedon.

G.

Galaesus, characters of, **229, 235.**
Galaesus hasticornis, **232, 233, 235, 236.**
Galago crassicaudatus, **177.**
Galago senegalensis, **177.**
gallegonis, Amblypelta.
Galleria mellonella, **323, 328, 337, 345.**
Gambia, pests of stored products in, **661, 667, 668.**
gambiae, Anopheles (*Myzomyia*).
Gambusia affinis, **459.**
garnhamellus, Anopheles rivulorum.
Gazelle, Grant's (*Gazella granti petersi*), *Hippobosca struthionis* and ticks on, **170.**

Gazelle, Thomson's, **533, 534.**
Gecko (see *Hemidactylus brookii*).
gediensis, Culex weschei.
Gelasima annulipes, **171.**
gelidus, Culex.
gemellatus, Lygus.
Genetta tigrina (Bush Genet), **427, 439.**
Geniocerus hagenowii (see *Tetrastichus*).
genurostris, Harpagomyia.
Geoskusea (see *Aëdes*).
germanica, Blattella.
Germany, *Lygus rugulipennis* in, **845.**
Giant Rat (see *Cricetomys gambianus*).
Giardia intestinalis, **140.**
Gibbium psylloides, **324, 328, 337, 345, 663.**
Gilbert Islands, mosquitos of, **291–300.**
gilletti, Eretmapodites.
Giraffe, **537.**
glauca, Pristiphora.
glebae, Cubitermes.
globulus, Trigonogenius.
gloriosae, Attagenus.
Glossina austeni, **159, 160, 162, 163, 168.**
Glossina brevipalpis, **159, 160, 162, 170.**
Glossina morsitans, **111**; pattern of populations of, **517–530**; host-animals of, **531–538**; measures against, **57–67, 589–597.**
Glossina pallidipes, **159, 160, 162, 168, 170, 521.**
Glossina palpalis, **111**; fertilisation of, in captivity, **357–368.**
Glossina swynnertoni, **521, 533, 537.**
glossinae, Mutilla; Syntomosphyrum.
Glossinella schillingsi (see *Lyperosia*).
Gnathocerus cornutus, **324, 328, 337, 345, 663.**
Gnathocerus maxillosus, **324, 328, 337, 345, 663.**
Gold Coast, *Aëdes albocephalus* in, **84**; pests and virus diseases of cacao in, **669–710**; *Pseudotheraptus devastans* in, **226, 227**; pests of stored products in, **644, 657, 661, 667.**
goliath, Macrotermes.
goliathi, Procubitermes.
Gongylonema neoplasticum, **140.**
Gonocephalum prolixum, **663.**
gracilis, Oxyuris.
grahami, Culex; Eretmapodites.
Grain Beetle, Flat (see *Laemophloeus minutus*).
Grain Beetle, Foreign (see *Ahasverus advena*).
Grain Beetle, Merchant (see *Oryzaephilus mercator*).
Grain Beetle, Red Rust (see *Laemophloeus ferrugineus*).
Grain Beetle, Saw-toothed (see *Oryzaephilus surinamensis*).
Grain Borer, Lesser (see *Rhizopertha dominica*).
Grain Moth, Angoumois (see *Sitotroga cerealella*).
Grain Weevil (see *Calandra granaria*).
Grain Weevil, Broad-nosed (see *Caulophilus latinasus*).
Grallatotermes africanus, **115, 116, 133.**
granaria, Calandra.
granarium, Trogoderma.
granella, Tinea.
granti, Aëdes (*Stegomyia*).
Grapefruit, fumigation of fruits of, against *Ceratitis capitata*, **804, 805, 806, 810.**
Graphiurus murinus, **427.**
Grapholitha (see *Cydia*).
Grass, Elephant (see *Pennisetum purpureum*).
gregaria, Schistocerca.
Gregarina blattarum, **140.**
grenieri, Uranotaenia.
grisella, Achroia.
Groundnut Beetle (see *Caryedon fuscus*).
Groundnuts, Stored, pests of, **643–668.**
Gryllodes sigillatus, **663.**
Grysbok, **59.**
Guam, *Ornithodoros capensis* in, **747.**
guiarti, Culex.
guineense, Tenebrio.
Gymnosporia, Ceroplastes destructor on, **267.**

H.

haddowi, Chimaeropsylla; Eretmapodites.
Haematopota crudelis, **159, 170.**
Haematopota maculosifacies, **159, 170.**
haemorrhoa, Protylocera.
haemorrhoidalis, Sarcophaga.
hagenowii, Tetrastichus (*Blattotetrastichus, Entedon, Geniocerus*).
halifaxii, Culex (*Lutzia*).
Hammerschmidtiella diesingi, **140.**
Hanane, **674.**
hancocki, Culex.
Harpagomyia, **69.**
Harpagomyia genurostris, **1.**
harperi, Eretmapodites.
Hartebeest, **59, 532, 533, 534, 536, 537.**
Hartebeest, Coke's, **518.**
hasticornis, Galaesus.
havilandi, Cryptotermes.
hawaiiensis, Holepyris.
haworthi, Aëdes (*Aëdimorphus*).
Hawthorn, *Thomasiniana* spp. on, **27, 28, 30, 31, 36.**

Hawthorn Stem Midge (see *Thomasiniana crataegi*).
hayashii, *Culex*.
hebetor, *Bracon*.
Hedgehog, African (see *Atelerix pruneri*).
heischi, *Aëdes* (*Stegomyia*).
Heliosciurus undulatus daucinus (see Squirrel).
Hemidactylus brookii, **426**, **511**, **512**.
hemipterus, *Carpophilus; Cimex*.
Heterobostrychus brunneus, **663**.
Heterohyrax syriacus diesneri (see Hyrax).
Heterospilus, **664**.
Hexamethonium, effect of, on isolated cockroach heart, **205–220**.
Hexamita periplanetae, **140**.
heydeni, *Thorictodes*.
Hide Beetle (see *Dermestes frischii*).
hilleri, *Pseudeurostus*.
Hippobosca capensis, **159**, **170**.
Hippobosca struthionis, **159**, **170**.
Hippopotamus, **59**.
Hippotragus equinus (see Antelope, Roan).
Hirstionyssus liberiensis, **159**, **170**.
hirsutus, *Aëdes* (*Aëdimorphus*).
hirta, *Mycetaea*.
hispida, *Ficalbia* (*Mimomyia*).
Hodotermes mossambicus, **114**, **118**, **124**.
Hofmannophila pseudospretella, **323**, **328**, **337**, **345**, **399–417**, **663**.
Holepyris hawaiiensis, **664**.
Holland, *Lygus rugulipennis* in, **845**.
holocinctus, *Aëdes* (*Aëdimorphus*) *cumminsi*.
hololeucus, *Niptus*.
Hop Trefoil (see *Medicago lupulina*).
Hormius, **908**, **909**.
Hornbill, Ground, **59**.
horrescens, *Aëdes* (*Stegomyia*).
horridus, *Culex* (*Neoculex*).
House Moth, Brown (see *Hofmannophila pseudospretella*).
Howardina (see *Aëdes*).
humanus, *Pediculus*.
Humidity, effects of: on development of insects, **788–794**, **869–898**; on toxicity of DDT deposits, **853–855**.
Hunting Dog (see *Lycaon*).
Hyaena, **535**, **536**.
Hygrocrocis intestinalis, **140**.
Hyperolius, **426**.
Hypophloeus, **663**.
Hyptia reticulata, **138**.
Hyrax (*Heterohyrax syriacus diesneri*, rock-rabbit), **427**, **429**, **430**, **433**, **434**, **438**, **439**, **508**, **509**, **510**, **511**, **512**, **514**, **515**, **532**, **533**, **534**.
hyrcanus, *Anopheles*.

I.

Impala, **518**, **532**, **534**.
imperfectus, *Pachynematus*.
implexus, *Anopheles*.
impressa, *Evania*.
impressicollis, *Diocalandra*.
inconspicuosus, *Culex* (*Mochthogenes*).
India, fruit moths in, **870**.
infantulus, *Culex* (*Lophoceraomyia*).
ingrami, *Aëdes* (*Finlaya*).
Inhibition Test, for identifying blood meals of *Glossina*, **533**, **534**.
inornatus, *Eretmapodites*.
Inostemma, **37**.
Insecticides, studies on aqueous suspensions of, **547–559**; physiological action of, on isolated cockroach heart, **205–220**.
Insects, cold-hardiness in, **311–355**, **813–835**; control values of percentage mortalities of, **189–191**.
insignis, *Culex* (*Neoculex*); *Tabanus*.
intermedius, *Eretmapodites*.
interpunctella, *Plodia*.
intestinalis, *Giardia*.
inunctus, *Tetrastichus*.
invidiosus, *Culex*.
Israel, *Anopheles sergentii* and malaria in, **445–462**; fumigation of *Citrus* fruits against *Ceratitis capitata* in, **803–811**; *Ornithodoros salahi* in, **747**.
Ixodes, **170**.
Ixodes schillingsi, **159**, **170**.

J.

Jackal, **533**, **535**, **536**.
Jalina, distinct from *Dasynus*, **236**.
Juan de Nova Island, mosquitos of, **104**.
Jugoslavia, *Ornithodoros lahorensis* in, **747**.

K.

kabaenensis, *Aëdes* (*Geoskusea*).
Kalotermes, **114**.
Kalotermes durbanensis, **114**, **116**, **117**, **122**.
Kalotermes kempae, **114**, **116**, **117**, **123**, **125**.
Kaolin, **633–639**.
kempae, *Kalotermes; Nasutitermes*.
keniensis, *Anopheles* (*Myzomyia*).
Kenya Colony, mosquitos in, **149–183**, **463–493**, **711–742**; other blood-sucking arthropods in, **158**, **159**, **160**, **162**, **163**, **168**, **170**; yellow fever in, **149**, **173**, **179**, **711**, **738**; Coccids on coffee, etc., in, **267–273**; Coreids in, **225**, **233**.

Khapra Beetle (see *Trogoderma granarium*).
kibarensis, Odontotermes.
kilimandjaricus, Anoplotermes.
Kingfisher, Black and White, **439.**
kingi, Culex argenteopunctatus.
kingianus, Culex.
Klipspringer, **59, 518.**
Kobus (see Waterbuck).
kochi, Aëdes (*Finlaya*).
Kudu, **533.**
kudvi, Plistophora.
kuehniella, Ephestia.
kunckeli, Protrellina.

L.

lacustris, Ficalbia (*Mimomyia*).
Ladybird, Seven Spot (see *Coccinella septempunctata*).
Laemophloeus, **400, 401, 402, 403, 413, 415, 644, 646, 648–651, 655, 656, 659, 660, 661, 665.**
Laemophloeus ferrugineus, **324, 328, 337, 345, 347, 405, 644, 650, 651, 653, 654, 657, 662.**
Laemophloeus minutus, **323, 324, 328, 337, 338, 345, 405, 644, 648, 650, 662.**
Laemophloeus pusilloides, **324, 328, 337, 338, 345, 346.**
Laemophloeus turcicus, **324, 328, 337, 338, 345, 348, 644, 663.**
Laemotmetus rhizophagoides, **663.**
laevigata, Evania.
laevigatus, Alphitobius.
lahorensis, Ornithodoros.
lamanianus, Schedorhinotermes.
lamborni, Aëdes (*Aëdimorphus*).
lamelliferus, Aëdes.
Lamprotatus, **37.**
lapponicus, Ectobius.
Larch, sawflies on, in Britain, **749–752.**
lardarius, Dermestes.
Larix (see Larch).
Lasioderma serricorne, **323, 324, 328, 338, 345, 347, 643–668.**
Laspeyresia molesta (see *Grapholitha*).
lateralis, Anoplotermes.
latericius, Odontotermes.
Latheticus oryzae, **324, 328, 338, 345, 405, 663.**
Lathridius bergrothi, **405.**
latinasus, Caulophilus.
latinotus, Ancistrotermes.
latipes, Pseudococcus.
Latrodectus mactans, **140.**
Laurel, persistence of DDT deposits on leaves of, **851, 853.**
lavandulae, Thomasiniana.
Lavia frons (see Bats).
lavieri, Uranotaenia.
Leather Beetle (see *Dermestes maculatus*).
Lecaniodiaspis erratica, sp.n., **269.**
leesoni, Aëdes (*Aëdimorphus*); *Anopheles* (*Myzomyia*).
Leidynema appendiculata, **140.**
Leopard, **533, 534.**
Lepisma saccharina, **323, 328, 338, 345, 348, 664.**
Leptacis, **37.**
leptolabis, Aëdes (*Aëdimorphus*).
Lettuce, not tainted by BHC, **919–920.**
Leucophaea surinamensis, **434.**
Leucoptera caffeina, bionomics of, on coffee in Tanganyika, **899–912.**
Leucoptera coffeella, **901–906.**
leucopterae, Elasmus.
leucopus, Eretmapodites.
Leurostenus filum, **663.**
liberiensis, Hirstionyssus.
Light, effects of, on reproduction in *Acyrthosiphon pisum,* **599–624.**
Light-traps, tests of efficiency of, **193–204.**
ligneus, Carpophilus.
lineatella, Anarsia.
lineatus, Aëdes.
Lion, **533, 534.**
livida, Ectobia.
Lizard, Agama (see *Agama atricollis*).
Lizard, Monitor (see *Varanus niloticus*).
Loa loa, **438.**
Loboptera decipiens, **138.**
Loboptera sakalava, **139.**
Locust, African Migratory (see *Locusta migratoria migratorioides*).
Locust, Desert (see *Schistocerca gregaria*).
Locusta migratoria migratorioides, method of marking scattered populations of, **797–802;** migration of solitary, **801.**
Loganberry, *Thomasiniana* spp. on, **28, 29, 36.**
longicornis, Chrysops.
longipalpis, Aëdes (*Finlaya*); *Anopheles; Mansonia.*
lonnbergianus, Amitermes.
Lophocateres pusillus, **663.**
Lophoceraomyia (see *Culex*).
Lophomonas blattarum, **140.**
Lophomonas striata, **140.**
Loxodonta africana (see Elephant).
Lucerne, *Acyrthosiphon pisum* on, **369–387, 389–392.**
lucyae, Uranotaenia.
ludlowae, Aëdes vigilax.
lungae, Anopheles (*Myzomyia*).

luteocephalus, Aëdes.
luteolus, Ceroplastes.
lutescens, Amblypelta; Toxorhynchites; Uranotaenia.
luteus, Microtermes.
Lutzia (see *Culex*).
Lycaon, **533.**
Lycophidion capensis, **426.**
Lyctocoris campestris, **401, 404, 662.**
Lyctus brunneus, **405.**
Lygus gemellatus, **846.**
Lygus lineolaris, **845.**
Lygus maritimus, **846.**
Lygus oblineatus (see *L. lineolaris*).
Lygus pratensis, species recorded as, **845–846.**
Lygus rugulipennis (*pubescens*), nomenclature and distribution of, **845–846;** bionomics of, in England, **846.**
Lygus rutilans, **846.**
Lyperosia schillingsi, **159, 170.**
Lyphia depressa, **663.**

M.

Mabuia striata, **426, 508, 511, 512.**
Macaca mulatta, **177.**
Macadamia ternifolia, *Amblypelta lutescens* on, **239.**
Macrotermes bellicosus, **115, 117, 118, 119, 130.**
Macrotermes goliath, **115, 117, 129, 130.**
macroura, Oxyuris.
mactans, Latrodectus.
maculatus, Anopheles; Callosobruchus; Carpophilus; Dermestes; Theraptus.
maculosifacies, Haematopota.
maculipalpis, Anopheles (*Myzomyia*).
maculipennis, Mansonia (*Coquillettidia, Taeniorhynchus*).
Madagascar, mosquitos in, **79, 84, 87, 88, 90, 95, 103, 104;** Coleoptera in stored beans in, **633.**
Mafia Island (see Tanganyika).
magnocellus, Microtermes.
mahaffyi, Eretmapodites.
Maize, Stored, pests in, **402, 403.**
Malaria (and mosquitos), in Israel, **445–462;** in New Hebrides and Solomon Is., **275–289.**
malariae, Plasmodium.
Malaya, mosquitos in, **301, 306, 307.**
malayi, Culex (*Mochthogenes*).
Maldive Islands, mosquitos of, **1–10, 104.**
Malt, *Trogoderma* spp. in, in Britain, **781, 785;** used for rearing *Trogoderma*, **788, 789, 790, 794.**
Manihot utilissima, *Pseudotheraptus devastans* on, **226, 239.**
mansoni, Oxyspirura.
Mansonia (*Taeniorhynchus*) *africanus*, **91, 158, 160, 161, 163, 169, 176, 177, 430, 440, 471, 495–515.**
Mansonia (*Taeniorhynchus*) *chrysosoma*, **158, 163, 470.**
Mansonia (*Taeniorhynchus*) *fuscopennatus*, **158, 163, 169.**
Mansonia longipalpis, **302, 304, 306.**
Mansonia (*Taeniorhynchus*) *maculipennis*, **158, 163, 169, 470.**
Mansonia (*Taeniorhynchus*) *metallicus*, **158, 163, 169, 430, 470.**
Mansonia (*Taeniorhynchus*) *uniformis*, **70, 78, 87, 91, 94, 100, 102, 158, 161, 163, 169, 177, 302, 304, 306, 431, 440, 471, 495–515.**
marginalis, Chrysomyia.
maritimus, Lygus.
Markhamia platycalyx, new Coccid on, **269.**
marshallensis, Aëdes (*Stegomyia*).
marshalli, Anopheles (*Myzomyia*).
masaiaticus, Microcerotermes.
mashonaensis, Uranotaenia.
mathesoni, Tripteroides (*Rachisoura*).
mauritanicus, Culex; Tenebroides.
Mauritius, mosquitos of, **104.**
maxillosus, Gnathocerus.
Meal Moth, Indian (see *Plodia interpunctella*).
Mealworm, Dark (see *Tenebrio obscurus*).
Mealworm, Lesser (see *Alphitobius diaperinus*).
Mealworm, Yellow (see *Tenebrio molitor*).
Medicago lupulina (Hop Trefoil), *Acyrthosiphon pisum* on, **369–387, 389–392.**
Medicago sativa (see Lucerne).
mediolineata, Ficalbia (*Etorleptiomyia*).
mediopunctatus, Aëdes (*Aëdimorphus*) *cumminsi.*
megatoma, Attagenus.
megatomoides, Trogoderma.
Melittobia chalybii, **138.**
mellonella, Galleria.
mercator, Oryzaephilus.
Mercurous Chloride, **23, 24, 25.**
Mestocharomyia oophaga, **138.**
metallica, Agamerion; Mansonia (*Coquillettidia, Taeniorhynchus*).
mettalicus, Aëdes (*Stegomyia*); *Taeniorhynchus* (see *Mansonia*).
Methyl Bromide, **402.**
Metophthalmus, **663.**
Mezium affine, **324, 328, 339, 345, 347, 663.**
michaelikati, Aëdes (*Dunnius*).
Microcerotermes, **114, 126, 133, 134.**

Microcerotermes brachygnathus, **114, 117, 125.**
Microcerotermes edentatus, **114, 116, 125.**
Microcerotermes masaiaticus, **114, 126.**
Microcerotermes parvulus, **114, 126.**
Microcerotermes parvus, **114, 117, 118, 119, 120, 125, 126, 127.**
Microlophium evansi, **562, 564, 565, 567, 584.**
Microtermes, **115, 132.**
Microtermes alluaudanus, **115, 117, 118, 119, 121, 132.**
Microtermes luteus, **115, 117, 118, 132.**
Microtermes magnocellus, **115, 119, 132.**
Microtermes redenianus, **115, 117, 118, 119, 121, 132.**
Microtermes vadschaggae, **115, 117, 118, 119, 120, 121, 132.**
migratoria, Locusta.
migratorioides, Locusta migratoria.
militaris, Pseudacanthotermes.
Mill Moth (see *Ephestia kuehniella*).
Mimomyia (see *Ficalbia*).
mimomyiaformis, Ficalbia (*Mimomyia*).
minutissimus, Culex (*Lophoceraomyia*).
minutus, Brachygaster; Dinoderus; Enicmus; Laemophloeus.
mirificus, Culex.
Mochthogenes (see *Culex*).
molesta, Cydia (*Grapholitha, Laspeyresia*).
molestus, Culex pipiens.
molitor, Tenebrio.
moluccensis, Anopheles punctulatus (see *A. farauti*).
Monanus concinnulus, **663.**
Mongoose, **533, 534.**
Mongoose, Marsh, **427, 439.**
Monkeys, **59, 518, 532, 534.**
Monomorium pharaonis, **664.**
Morocco, *Ornithodoros coniceps* in, **747.**
morogorensis, Allodontermes.
morsitans, Glossina.
Mortality Percentages, relative control values of, **189–191.**
Mosquitos, in Kenya, **463–493**; of Maldive Islands, **1–10, 104**; in Pacific islands, **275–289, 291–300**; of Seychelles, **69–110**; in Tanganyika, **419–436, 437–444, 495–504, 505–515**; traps for, **451–455**; susceptibility of, to insecticides, **301–309.** (See also under *Aëdes*, *Anopheles* and *Eretmapodites*).
mossambicus, Hodotermes.
moubata, Ornithodoros.
moucheti, Culex.
moultoni, Uranotaenia.
Mouse, **532.**
mucidus, Aëdes (*Mucidus*).
Mud Blocks, sorption of DDT by, **547–559.**
multicolor, Anopheles.
munroi, Plastanoxus.
muricola, Protospirura.
Murmidius segregatus, **663.**
musarum, Culex.
Musca domestica, **434.**
Musca domestica nebulo, **111.**
Musca nebulo (see *M. domestica nebulo*).
Mussidia nigrivenella, **663.**
Mustard Beetle (see *Phaedon cochleariae*).
Mutilla glossinae, **111.**
Mycetaea hirta, **663.**
Mycetophagus, **663.**
Mycetophagus quadriguttatus, **405.**
Myzomyia (see *Anopheles*).

N.

Naja nigricollis, **426.**
Nasturtium officinale (see Watercress).
Nasutitermes kempae, **115, 133.**
Nasutitermes usambarensis, **115, 116, 119, 133.**
natronius, Aëdes (*Aëdimorphus*).
neavei, Culex univittatus.
nebulo, Musca domestica.
nebulosus, Culex (*Culiciomyia*).
Necrobia ruficollis, **661, 662.**
Necrobia rufipes, **323, 328, 339, 345, 643–668.**
Necrobia violacea, **663.**
Nemeritis canescens, **664.**
Neoculex (see *Culex*).
neoplasticum, Gongylonema.
Neostylopyga (*Dorylaea*) *rhombifolia*, **138, 663.**
Neotermes, **114, 116, 123.**
nepenthes, Uranotaenia.
nepenthis, Tripteroides.
Nettle, Aphids and Coccinellids on, **561–587.**
Nettle Aphid (see *Microlophium evansi*).
New Hebrides, mosquitos and malaria in, **275–289.**
ngong, Aëdes (*Aëdimorphus*).
Nicotine, effect of, on isolated cockroach heart, **205–220.**
Nigeria, *Culex simpsoni* in, **86**; parasite of cockroaches in, **111–112**; *Pseudotheraptus devastans* on *Manihot utilissima* in, **226**; *Glossina palpalis* in, **357, 362**; pests of stored products in, **644, 649, 650, 657, 659, 661, 664, 665, 667.**
nigeriensis, Aëdes (*Ochlerotatus*) (see *A. fryeri*).

nigerrimus, Aëdes (*Mucidus*).
nigricana, Cydia.
nigripes, Uranotaenia.
nigrivenella, Mussidia.
nigromarginatus, Dasynus (*Pendulinus, Theraptus*).
nili, Anopheles (*Myzomyia*).
Niptus hololeucus, **324, 328, 339, 345.**
Nitrogen Trichloride (see Decco).
njalensis, Pseudococcus.
nocturnus, Aëdes (*Aëdimorphus*) *vexans.*
Noditermes, **115, 118, 119, 128.**
Nor-adrenaline, effect of, on isolated cockroach heart, **205–220.**
Nosema apis, in bees in Britain, **753–759.**
Nosopsyllus, **405.**
nummatus, Aëdes.
Nycteris hispida (see Bats).
Nyctotherus ovalis, **140.**

O.

Oats, Stored, pests in, and their control, **401, 402, 403.**
oblineatus, Lygus (see *L. lineolaris*).
obsoletus, Carpophilus; Cryptophagus.
obscura, Acanthaspis.
obscurus, Tenebrio.
obtectus, Acanthoscelides.
obturbans, Armigeres.
Ochlerotatus (see *Aëdes*).
ochraceus, Aëdes (*Aëdimorphus*).
oculiperda, Thomasiniana.
Odontoparia, doubtfully distinct from *Dasynus*, **236.**
Odontotermes, **115, 132, 134.**
Odontotermes amanicus, **115, 119, 130.**
Odontotermes amaniensis, **115, 130.**
Odontotermes badius, **115, 119, 120, 130.**
Odontotermes boranicus, **115, 131.**
Odontotermes culturarum, **115, 117, 119, 131.**
Odontotermes kibarensis, **115, 131.**
Odontotermes latericius, **115, 118, 119, 131, 134.**
Odontotermes patruus, **115, 131.**
Odontotermes rectanguloides, **115, 117, 119, 120, 131.**
Odontotermes stercorivorus, **115, 121, 131.**
Odontotermes tanganicus, **115, 117, 131.**
Odontotermes zambesiensis, **115, 118, 119, 132.**
oedipodius, Eretmapodites.
Oil Palm, pests of stored kernels of, **647–653, 655, 657, 658, 659, 667, 668.**
oleisuga, Thomasiniana (*Clinodiplosis*).
Oncocephalus, **158, 163.**
Onion, Anthomyiid flies on, in Britain, **11, 21–26.**
Onion Fly (see *Delia antiqua*).
Onobrychis sativa (see Sainfoin).
oophaga, Mestocharomyia.
Orange, fumigation of fruits of, against *Ceratitis capitata*, **803–811.**
Oreotragus oreotragus (see Klipspringer).
orientalis, Blatta.
ornata, Uranotaenia.
ornatothoracis, Culex.
Ornithodoros, distribution of Old World species of, **747–748.**
Ornithodoros arenicolous, **747.**
Ornithodoros capensis, **747.**
Ornithodoros coniceps, **747.**
Ornithodoros delanoei, **747.**
Ornithodoros erraticus, **747.**
Ornithodoros foleyi, **747.**
Ornithodoros lahorensis, **747.**
Ornithodoros moubata, **435.**
Ornithodoros salahi, **747.**
Ornithodoros savignyi, doubtfully occurring in Belgian Congo, **748.**
Ornithodoros tartakovskyi, **747.**
Ornithodoros tholozani, **747.**
Ornithodoros zumpti, **747.**
Orphinus fulvipes, **663.**
Orthopodomyia arboricolis, **104.**
oryzae, Calandra; Latheticus.
Oryzaephilus, **643–668.**
Oryzaephilus mercator, **324, 328, 339, 345, 347, 644, 662.**
Oryzaephilus surinamensis, **324, 328, 339, 345, 347, 401, 402, 403, 405, 410, 412, 413, 644, 662.**
ovalis, Nyctotherus.
ovatum, Balantidium.
ovivora, Systellogaster.
Oxyspirura mansoni, **140.**
Oxyuris gracilis, **140.**
Oxyuris macroura, **140.**

P.

Pachynematus imperfectus, **751.**
Paint, for marking locusts, **798, 799, 800, 801.**
Pakistan, fruit moths in, **870.**
pallens, Plochionus.
pallescentella, Tinea.
pallida, Ficalbia (*Mimomyia*).
pallidipes, Glossina.
pallidothorax, Culex.
Palorus, **663, 665.**
Palorus ratzeburgi, **324, 328, 339, 340, 345, 346, 663.**

Palorus subdepressus, **324, 328, 339, 340, 345, 346, 663.**
palpalis, Glossina.
paludis, Anopheles.
pandani, Uranotaenia.
paniceum, Stegobium.
Papio (see Baboon).
papuensis, Aëdes (Finlaya); Culex (Culiciomyia).
par, Tabanus.
Paradasynus, **236.**
Paraëdes argyrurus, **85.**
parainfantulus, Culex (see *C. infantulus*).
Paraoxon, **673–677, 682, 683, 702**; effect of, on isolated cockroach heart, **205–220.**
Parathion, **673–677, 682, 683, 702**; effect of, on isolated cockroach heart, **205–220.**
Parcoblatta pensylvanica, **138.**
Parcoblatta virginica, **139.**
Paris Green, **459.**
parvipluma, Eretmapodites oedipodius.
parvum, Treponema.
parvulus, Microcerotermes.
parvus, Microcerotermes.
Passalactis tentatrix (see *Plastopolypus*).
Passer domesticus (see Sparrow).
patruus, Odontotermes.
pauliani, Uranotaenia (see *U. pandani*).
Pea, *Acyrthosiphon pisum* on, **369–387.**
Pea, Stored, dusts against Bruchids in, **625–641.**
Pea Aphid (see *Acyrthosiphon pisum*).
Pea Moth (see *Cydia nigricana*).
Peach, *Thomasiniana oculiperda* ovipositing on, **29**; *Cydia molesta* on, **870–871.**
Peach Moth, Oriental (see *Cydia molesta*).
Peach Tip Moth (see *Cydia molesta*).
Peach Twig Borer (see *Anarsia lineatella*).
Peach Worm, Oriental (see *Cydia molesta*).
Pear, *Thomasiniana oculiperda* ovipositing on, **29.**
Pear Borer, Smaller (see *Cydia molesta*).
pectinicornis, Rhipidius.
Pediculus humanus capitis, **435.**
pellio, Attagenus.
pellionella, Tinea.
pellucidum, Ellipsidion.
Pelusios sinuatus, **426.**
Pemba, new Coreid in, **221, 224, 225.**
pembaensis, Aëdes (Skusea).
Pendulinus carmelita (see *Theraptus*).
Pendulinus devastans (see *Pseudotheraptus*).
Pendulinus hasticornis (see *Galaesus*).
Pendulinus nigromarginatus (see *Dasynus*).
penicillatus, Eretmapodites.
Pennisetum purpureum, arthropod population of the soil under, in Uganda, **539–545.**
pensylvanica, Parcoblatta.
Pentarthrum cylindricum, **663.**
perexiguus, Culex (see *C. univittatus*).
perfuscus, Culex.
Pericapritermes dumicola, **115, 118, 129.**
Perilitus coccinellae, **572.**
Periplaneta americana, **323, 328, 345, 663**; parasites and predators of, **111–112, 137–147**; used for tests of action of drugs and insecticides, **205–220, 837–843.**
Periplaneta australasiae, **663**; parasites and predators of, **137–147.**
periplanetae, Coelosporidium; Hexamita; Tetrastichus.
perkinsi, Culex (Acallyntrum).
Persia, *Ornithodoros tartakovskyi* in, **747.**
perstans, Acanthocheilonema.
Petrodromus sultani sultani, Ctenocephalides felis and ticks on, **170.**
Phacochoerus aethiopicus (see Warthog).
Phaedon cochleariae, effect of diet on egg-production in, **393–397.**
Pharaoh's Ant (see *Monomorium pharaonis*).
pharaonis, Monomorium.
pharoensis, Anopheles (Myzomyia).
Philantomba caerulea (see Duiker, Blue).
Philothamnus semivariegatus, **426, 512, 513.**
Photoperiod (see Light).
Phyllodromia, **139.**
piceus, Alphitobius (see *A. laevigatus*); *Attagenus* (see *A. megatoma*).
picticornis, Solendenia (Anastatus).
Piestopleura catillus, **37.**
Pigeon, **439.**
pilosus, Cryptophagus.
Pimeliaphilus podapolipophagus, **140.**
Piramurana, distinct from *Dasynus*, **236.**
pipiens, Culex pipiens.
pisum, Acyrthosiphon.
Plagiostoma blattarum, **140.**
planifacies, Procubitermes.
planifrons, Reduvius.
Plant Wax, persistence of DDT deposits on, **39–56, 849–868.**
Plasmodium, **275, 278, 283.**
Plasmodium falciparum, **278, 281, 282, 284, 445.**
Plasmodium malariae, **277, 278, 280, 281, 282, 283.**

Plasmodium vivax, **277**, **278**, **280–284**.
Plastanoxus munroi, **664**.
Plastanoxus westwoodi, **664**.
Plastopolypus tentatrix, **124**.
Platymeris erebus, **158**, **170**.
Platynectes, **277**.
Pleurotropis coffeicola, **907**, **908**, **909**.
Plinachtus, characters of, **231**, **237**, **238**, **239**.
Plinachtus pugionatus, **238**.
Plinachtus pungens, **233**, **235**.
Plinachtus spinosus, **221**, **222**, **227**, **228**, **234**, **235**, **236**.
plioleuca, *Eretmapodites*.
Plistophora kudvi, **140**.
Plochionus pallens, **663**.
Plodia interpunctella, **323**, **328**, **340**, **345**, **347**, **400–403**, **405**, **643–668**, **831**.
Plum, *Thomasiniana oculiperda* ovipositing on, **29**.
plumosa, *Ficalbia* (*Mimomyia*).
podapolipophagus, *Pimeliaphilus*.
poicilipes, *Culex*.
polynesiensis, *Aëdes* (*Stegomyia*).
pomonella, *Cydia* (*Carpocapsa*).
Porcupine, **532**, **533**, **534**.
Potamochoerus porcus (see Bushpig).
Potato, tainted by BHC, **919–920**.
praenucleatum, *Balantidium*.
pratensis, *Lygus*.
Precipitin Test, for identifying blood meals of insects, **506**, **509**, **510**, **531**, **534**.
Pristiphora glauca, larval characters and bionomics of, on larch in Britain, **749–752**.
Pristiphora wesmaeli, **749**.
Procavia, **59**.
Procryptotermes, **114**, **123**.
Procryptotermes angulatus, **119**.
Procubitermes goliathi, **115**.
Procubitermes planifacies, **115**, **128**.
productus, *Eretmapodites leucopus*.
Prolabia arachidis, **664**.
prolixum, *Gonocephalum*.
Promirotermes bellicosi, **115**, **117**, **129**.
Propylea quatuordecimpunctata, **562**, **567–572**, **574**, **577**, **580**.
Protospirura muricola, **140**.
Protrellina australasiae, **140**.
Protrellina kunckeli, **140**.
Protylocera haemorrhoa, **434**.
Prunus spinosa (see Blackthorn).
Pseudacanthotermes militaris, **115**, **117**, **129**.
Pseudeurostus hilleri, **324**, **328**, **340**, **345**.
pseudocinereus, *Culex nebulosus*.
Pseudococcus latipes, sp.n., **271**.
Pseudococcus njalensis, **271**; insecticides against, on cacao in Gold Coast, **669–710**.
Pseudoficalbia (see *Uranotaenia*).
Pseudopendulinus, **236**.
pseudoscutellaris, *Aëdes* (*Stegomyia*).
pseudospretella, *Hofmannophila*.
Pseudotheraptus, gen.n., **222**; related genera compared with, **229–239**; key to species of, **229**.
Pseudotheraptus (*Theraptus*) *devastans*, **221–240**.
Pseudotheraptus ugandae, sp.n., **221**, **222**, **226**, **227–229**, **233**, **234**, **235**, **239**.
Pseudotheraptus wayi, sp.n., identity and systematic position of, on coconut in East Africa, **221–240**; type of genus, **223**.
psylloides, *Gibbium*.
Pteromalus, **139**.
Ptinus, **408**, **410**, **411**, **413**, **414**, **415**.
Ptinus fur, **324**, **328**, **340**, **345**, **346**, **401**, **405**.
Ptinus pusillus, **405**.
Ptinus sexpunctatus, **324**, **328**, **340**, **345**, **346**.
Ptinus tectus, **324**, **328**, **340**, **345**, **346**, **400–404**.
pubescens, *Lygus* (see *L. rugulipennis*).
pugionatus, *Plinachtus*.
Puku (see *Adenota vardoni*).
pulchellus, *Rhipicephalus*.
pullus, *Culex* (*Culiciomyia*).
punctata, *Evania*.
punctatum, *Anobium*.
punctulatus, *Anopheles* (*Myzomyia*).
pungens, *Plinachtus*.
pusilloides, *Laemophloeus*.
pusillus, *Lophocateres*; *Ptinus*.
putoria, *Chrysomyia*.
Pyralis farinalis, **404**, **663**.
Pyrethrins (or Pyrethrum), **400**, **401**, **438**, **439**, **440**; effect of, on isolated cockroach heart, **205–220**.
Pyrus, *Thomasiniana oculiperda* on, **36**. (See Apple and Pear).
Python sebae, **426**.

Q.

quadricollis, *Cathartus*.
quadriguttatus, *Mycetophagus*.
quadrimaculata, *Uranotaenia*.
quadrimaculatus, *Anopheles*.
quasiguiarti, *Culex*.
quattuordecimstriata, *Carcinops*.
quatuordecempunctata, *Propylea*.
queenslandensis, *Aëdes aegypti*.
Quince, *Thomasiniana oculiperda* not ovipositing on, **29**.
quinquemaculata, *Uranotaenia*.
quinquevittatus, *Eretmapodites*.

R.

Rachisoura (see *Tripteroides*).
Rana occipitalis, **426, 439, 511, 512.**
rapae, *Trybliographa.*
Raphicerus sharpei (see Grysbok).
rapulum, *Trinervitermes.*
Raspberry, *Thomasiniana* spp. on, **27–32.**
Raspberry Cane Midge (see *Thomasiniana theobaldi*).
Rat, Black (see *Rattus rattus*).
Rat, Multimammate (see *Rattus coucha*).
Rats, **98, 427, 439, 511, 512, 532, 533, 534.**
Rattus coucha, **427, 439, 511, 512.**
Rattus rattus, **98, 427.**
ratzeburgi, *Palorus.*
Ravenalites, **69.**
rectanguloides, *Odontotermes.*
redenianus, *Microtermes.*
Redunca arundinum (see Reedbuck).
Redunca redunca (see Reedbuck, Bohor).
Reduvius, **663.**
Reduvius planifrons, **158, 170.**
Reedbuck, **59, 532–536.**
Reedbuck, Bohor, **518.**
Reedomyia (see *Aëdes*).
reticulata, *Hyptia.*
Retortamonas blattae, **140.**
Réunion, mosquitos in, **104.**
Rhabdomys pumilio, **747.**
rhecter, *Aëdes.*
Rhinoceros, **518, 519, 532, 535, 536.**
Rhinonax chrysopygus, flea and tick on, **170.**
Rhipicephalus appendiculatus, **159, 170.**
Rhipicephalus pulchellus, **159, 170.**
Rhipicephalus sanguineus, **159, 170.**
Rhipicephalus simus, **159, 170.**
Rhipidius pectinicornis, **139.**
Rhizopertha dominica, **322, 323, 324, 328, 341, 345, 347, 401, 402, 403, 405, 662, 663.**
rhizophagoides, *Laemotmetus.*
Rhodesia, Northern, *Glossina morsitans* in, **57–67.**
rhodesiense, *Trypanosoma.*
rhodesiensis, *Anopheles* (*Myzomyia*).
rhombifolia, *Neostylopyga* (*Dorylaea*).
Rhynchotragus kirkii (see Dikdik).
rhytipleurites, *Filaria.*
Ribes alpinum, *Thomasiniana* sp. on, **27.**
Rice Moth (see *Corcyra cephalonica*).
Rice Weevil (see *Calandra oryzae*).
riveroi, *Thelastoma.*
rivulorum, *Anopheles* (*Myzomyia*).
robici, *Culex.*
Robin, **583.**
Rock Phosphate, **633, 634, 635, 638.**
Rock-rabbit (see *Hyrax* and *Procavia*).
Rose (*Rosa canina*), *Thomasiniana* spp. on, **27–32, 36.**
Rotenone, effect of, on isolated cockroach heart, **205–220.**
rubithorax, *Aëdes.*
Rubus spp. (see Blackberry).
ruficollis, *Ampulex;* *Necrobia.*
rufipes, *Anopheles;* *Necrobia.*
rugulipennis, *Lygus.*
rusticus, *Aëdes* (*Ochlerotatus*).
rutilans, *Lygus.*
ruwenzori, *Aëdes* (*Stegomyia*).

S.

saccharina, *Lepisma.*
sacharovi, *Anopheles.*
saginatus, *Cryptophagus.*
Sainfoin, *Acyrthosiphon pisum* on, **369, 370, 379, 380.**
sakalava, *Loboptera.*
salahi, *Ornithodoros.*
salvadorae, *Thomasiniana.*
samoanus, *Anopheles* (*Finlaya*).
sanguineus, *Rhipicephalus.*
sarcitrella, *Endrosis.*
Sarcophaga haemorrhoidalis, **111.**
savignyi, *Ornithodoros.*
scatophagoides, *Aëdes* (*Mucidus*).
Scenopinus fenestralis, **405, 408, 410–414, 416.**
Schedorhinotermes lamanianus, **114, 116, 119, 124.**
schillingsi, *Ixodes;* *Lyperosia* (*Glossinella*).
Schistocerca gregaria, **799.**
schneideri, *Diplocystis.*
Schradan, **673, 674, 677, 682.**
scotti, *Culex.*
scutellaris, *Aëdes* (*Stegomyia*).
Scymnus, **700.**
Seed Beetle, American (see *Acanthoscelides obtectus*).
segelli, *Trinervitermes.*
segregatus, *Murmidius.*
seldeslachtsi, *Culex.*
semibrunneus, *Culex* (*Culiciomyia*).
semisimplicipes, *Eretmapodites.*
Senegal, *Culex simpsoni* in, **86;** pests of stored products in, **655, 664.**
septempunctata, *Coccinella.*
sergentii, *Anopheles* (*Myzomyia*).
sericea, *Evania.*
serricorne, *Lasioderma.*
Sesarma spp. (see Crabs).
sexpunctatus, *Ptinus.*
seychellensis, *Reedomyia* (see *Aëdes albocephalus*).

Seychelles, mosquitos of, **69–110.**

Shelfordella tartara, **139.**

Shell Risella Oil 17, **301.**

Shrew, Elephant (see *Petrodromus* and *Rhinonax*).

Siam, *Aëdes vigilax* in, **87, 90.**

siberica, Ampulex (see *A. compressiventris*).

Sierra Leone, pests of stored products in, **644, 657, 661, 667.**

sigillatus, Gryllodes.

Silica, **633, 634, 635, 638, 639.**

Silvanus unidentatus, **663.**

Silverfish (see *Lepisma saccharina*).

silvestris, Eretmapodites.

similis, Allacta.

simpsoni, Aëdes (*Stegomyia*); *Culex.*

simus, Rhipicephalus.

sinaiticus, Culex.

Sinoxylon anale, **663.**

Sisal Wax, persistence of DDT deposits on, **42–47.**

sitiens, Culex.

Sitotroga cerealella, **323, 328, 341, 345, 347, 402, 405, 662, 663.**

Skink, Grant's (see *Mabuia striata*).

Skusea (see *Aëdes*).

Sleeping Sickness, **519, 537.**

Socotra Island, mosquitos of, **104.**

Soil, arthropod population of, under elephant grass in Uganda, **539–545;** studies on sorption of insecticides by blocks of, **547–559.**

soleatus, Aëdes (*Stegomyia*).

Solendenia blattiphagus (see *Anastatus blattidarum*).

Solendenia picticornis, **138.**

Solomon Islands, mosquitos and malaria in, **275–289.**

solomonis, Anopheles (*Myzomyia*).

sonnerati, Ampulex.

sordidus, Aphanus.

soror, Cutilia.

Sparrow, **583.**

spathifurca, Culex (*Culiciomyia*).

Sphenorhynchus abdimii, **59.**

Spider Beetle, African (see *Stethomezium squamosum*).

Spider Beetle, Australian (see *Ptinus tectus*).

Spider Beetle, Globular (see *Trigonogenius globulus*).

Spider Beetle, Golden (see *Niptus hololeucus*).

Spider Beetle, Hump (see *Gibbium psylloides*).

Spider Beetle, Japanese (see *Pseudeurostus hilleri*).

Spider Beetle, White-marked (see *Ptinus fur*).

Spiniger domesticus, **139.**

spinosus, Plinachtus.

Spirillum, **140.**

splendens, Ficalbia (*Mimomyia*).

splendidula, Zeuxevania.

Spray Gun, for marking locusts in the field, **797–802;** for applying DDT deposits to leaves, **850–851.**

squamosum, Stethomezium.

squamosus, Anopheles (*Myzomyia*); *Culex.*

Squirrel, *Hirstionyssus liberiensis* on, **170.**

Staphylococcus albus, **140.**

Stegobium paniceum, **324, 328, 341, 345, 348, 644, 663.**

Stegomyia (see *Aëdes*).

stellatus, Culex (*Neoculex*).

stercorea, Typhaea.

stercorivorus, Odontotermes.

Stethomezium squamosum, **324, 328, 341, 345.**

stokesi, Aëdes (*Aëdimorphus*).

Stomoxys calcitrans, **434.**

Stork (see *Sphenorhynchus* and *Ciconia*).

Strawberry, persistence of DDT deposits on leaves of, **852, 853.**

striata, Lophomonas.

struthionis, Hippobosca.

stylifurcatus, Culex (see *C. spathifurca*).

stylopygae, Treponema.

subargenteus, Aëdes (*Stegomyia*).

subdepressus, Palorus.

subfasciatus, Zabrotes.

subpictus, Anopheles (*Myzomyia*).

subruber, Withius.

subsimplicipes, Eretmapodites.

subspinosa, Evania.

Sudan, identity of common *Trogoderma* in, **773–775.**

Sudan, French, *Locusta migratoria migratorioides* in, **797–802.**

Sulphonated Lorol, **851, 855.**

Sulphur, **633.**

sumatranus, Culex.

Supella supellectilium, **138.**

superpictus, Anopheles (*Myzomyia*).

surinamensis, Leucophaea; Oryzaephilus.

Sweden, *Lygus rugulipennis* in, **845.**

swynnertoni, Glossina.

Sylvicapra grimmia (see Duiker).

Symbius blattarum (see *Rhipidius pectinicornis*).

Synacanthotermes zanzibarensis, **115, 117, 128, 129.**

Syncerus caffer (see Buffalo).

Syntomosphyrum glossinae, parasitising cockroach oothecae, **111–112;** hosts and distribution of, **111.**

Systellogaster ovivora, **139.**

T.

Tabanus fraternus, **159**, **170**.
Tabanus insignis, **159**, **163**.
Tabanus par, **159**, **170**.
Tabanus taeniola, **159**, **170**, **434**.
Tabanus thoracinus, **159**, **170**.
taeniola, *Tabanus*.
Taeniorhynchus (see *Mansonia*).
Talc, **633**, **634**, **635**, **638**.
tanganicus, *Odontotermes*.
Tanganyika Territory, *Glossina* spp. in, **111**, **517–530**, **531–538**, **589–597**; mosquitos and filariasis in, **419–436**, **437–444**, **495–504**, **505–515**; termites of, **113–135**; *Leucoptera caffeina* on coffee in, **899–912**; new Coreid on coconut, etc., in, **225**; *Acanthoscelides obtectus* in stored beans in, **627**.
Tapestry Moth (see *Trichophaga tapetzella*).
tapetzella, *Trichophaga*.
Taphozous mauritianus (see Bats).
Tarnished Plant Bug, American (see *Lygus lineolaris*).
Tarnished Plant Bug, European (see *Lygus rugulipennis*).
tarsalis, *Aëdes* (*Aëdimorphus*).
tartakovskyi, *Ornithodoros*.
tartara, *Shelfordella*.
Taurotragus oryx (see Eland).
taylori, *Aëdes* (*Diceromyia*).
tectus, *Ptinus*.
teesdalei, *Aëdes* (*Aëdimorphus*).
Temperature, effects of: on development and fecundity of insects, **599–624**, **781**, **784**, **788–794**, **869–898**; on toxicity of DDT, **855–866**. (See Cold-hardiness.)
Tendipes, **297**.
Tenebrio guineense, **663**.
Tenebrio molitor, **324**, **328**, **341**, **342**, **345**, **347**, **399–417**, **663**.
Tenebrio obscurus, **324**, **328**, **341**, **342**, **345**, **347**.
Tenebroides mauritanicus, **324**, **328**, **342**, **345**, **400–403**, **405**, **408**, **410**, **413**, **414**, **643–668**.
tenebrosus, *Anopheles coustani*.
tentatrix, *Plastopolypus* (*Passalactis*).
Termites, of north-eastern Tanganyika, **113–135**; methods of estimating abundance of subterranean, **120–122**.
Terrapin, Natal (see *Pelusios sinuatus*).
tessellatus, *Anopheles* (*Myzomyia*).
Tetrastichus australasiae, **138**.
Tetrastichus hagenowii (*browni*, *floridanus*), bionomics of, **140–145**.
Tetrastichus inunctus, **37**.
Tetrastichus periplanetae, **138**.
thalassius, *Culex*.
Thaneroclerus buqueti, **662**.
theileri, *Culex*.
Thelastoma bulhoesi, **140**.
Thelastoma riveroi, **140**.
theobaldi, *Thomasiniana*.
Theobroma cacao (see Cacao).
Theraptus, systematic position of, **221**, **222**, **229**, **231–234**; key to species of, **233–234**.
Theraptus carmelita, **222**, **227**, **228**, **230–236**.
Theraptus devastans (see *Pseudotheraptus*).
Theraptus distanti (see *Dasynus*).
Theraptus maculatus, **227**, **230**, **232**, **233**, **234**.
Theraptus nigromarginatus (see *Dasynus*).
Thermobia domestica, **664**.
tholozani, *Ornithodoros*.
Thomasiniana, host-plant preferences of species of, in Britain, **27–38**.
Thomasiniana crataegi, **27**, **30–34**, **36**, **37**.
Thomasiniana fruticosi, sp.n., **34–37**.
Thomasiniana lavandulae, **27**.
Thomasiniana oculiperda, **27**, **30–34**, **36**, **37**.
Thomasiniana oleisuga, **27**.
Thomasiniana salvadorae, **27**.
Thomasiniana theobaldi, **27**, **28**, **29**, **31**, **32**, **33**, **34**, **36**, **37**.
thomsoni, *Endamoeba*.
thoracinus, *Tabanus*.
Thorictodes heydeni, **663**, **665**.
tigripes, *Culex* (*Lutzia*).
Tilapia, **459**.
Tinea columbariella, **323**, **328**, **330**, **345**, **663**.
Tinea granella, **323**, **328**, **342**, **345**, **401**, **405**, **663**.
Tinea pallescentella, **404**.
Tinea pellionella, **323**, **328**, **330**, **345**, **347**, **663**.
Tineola bisselliella, **323**, **328**, **342**, **345**, **347**, **663**.
Tipnus unicolor, **402**, **405**.
Toad, African (see *Bufo regularis*).
Tobacco Moth (see *Ephestia elutella*).
Togo, pests of stored products in, **667**.
Tokelau Islands, mosquitos and filariasis in, **291–300**.
Tonga, abnormal mosquito larvae in, **185–188**.
tonsus, *Eretmapodites*.
Topomyia, **77**.
Toxorhynchites, **173**.
Toxorhynchites (*Megarhinus*) *brevipalpis*, **158**, **172**, **467**.

Toxorhynchites lutescens, **467.**
Tragelaphus scriptus (see Bushbuck).
Traps, for mosquitos, **451–455.** (See Light-traps.)
Tree Frog (see *Hyperolius*).
Tree Snake, Green (see *Philothamnus semivariegatus*).
Treponema parvum, **140.**
Treponema stylopygae, **140.**
Tribolium, **643.**
Tribolium anaphe, **663.**
Tribolium castaneum, **43, 322, 324, 328, 342, 343, 345, 346, 347, 401, 402, 403, 405, 413, 415, 416, 643–668;** used in tests of toxicity of DDT, **852–855, 858, 862, 863, 864.**
Tribolium confusum, **323, 324, 328, 343, 345, 645, 646, 653, 654, 655, 660, 662, 664, 665.**
Tribolium destructor, **324, 328, 343, 345, 663.**
trichodactyla, *Delia*.
tricholabis, *Aëdes* (*Aëdimorphus*).
Trichophaga tapetzella, **323, 328, 343, 345.**
trifoliatus, *Culex*.
Trigonogenius globulus, **324, 328, 343, 345, 402, 405.**
Trimorus, **37.**
Trinervitermes, **115, 117, 118, 120, 125, 126, 132, 134.**
Trinervitermes bettonianus, **115, 134.**
Trinervitermes rapulum, **115, 133.**
Trinervitermes segelli, **115, 133.**
Trinidad, parasite of cockroaches in, **142.**
Tripteroides, **77, 85, 277, 285, 288.**
Tripteroides coeruleocephala, **85.**
Tripteroides mathesoni, **280, 281, 285, 288.**
Tripteroides nepenthis, **85.**
tritaeniorhynchus, *Culex*.
Trogoderma, **643, 651, 652, 655, 656, 659, 661, 668.**
Trogoderma granarium (*afrum*), **324, 328, 343, 345, 347, 348, 644, 645, 646, 654, 657, 660, 662, 664;** bionomics of, **781–796;** characters and synonymy of, **773–780.**
Trogoderma inclusum, **773.**
Trogoderma megatomoides, **781.**
Trogoderma versicolor, **324, 328, 344, 345, 347, 644, 663;** bionomics of, **781–796;** characters and synonymy of, **773–780.**
truncatus, *Angulitermes*.
Trybliographa rapae, **15.**
Trypanosoma rhodesiense, **519.**
Trypanosoma vivax, **64.**
Trypanosomiasis, in cattle, **59, 64.**
tsaratananae, *Uranotaenia*.
Tsetse Flies (see *Glossina*).
tubanguii, *Uranotaenia*.
Tunga, **435.**
turcicus, *Laemophloeus*.
Turkey, *Ornithodoros* spp. in, **747.**
Turnip Root Fly (see *Erioischia floralis*).
Typhaea stercorea, **405, 663.**
Tyroglyphus farinae, **401, 402, 403.**

U.

Uganda, Coccids on coffee in, **267–273;** new Coreid in, **222, 227–228;** *Dysdercus* spp. in, **743;** *Eretmapodites* spp. in, **761–772;** soil arthropod population under elephant grass in, **539–545.**
ugandae, *Pseudotheraptus*.
Ukara Island (see Tanganyika).
umbraticola, *Crenetermes*.
umbratus, *Cubitermes*.
undecimpunctata, *Coccinella*.
unicolor, *Tipnus*.
unidentatus, *Amitermes; Silvanus*.
uniformis, *Ficalbia* (*Mimomyia*); *Mansonia* (*Coquillettidia*, *Taeniorhynchus*).
Union of Soviet Socialist Republics, *Lygus* spp. in, **845.**
United States of America, *Cydia molesta* (Oriental Fruit Moth) in, **870–871.**
univittatus, *Culex*.
Uranotaenia alboabdominalis, **430, 467.**
Uranotaenia ascidiicola, **75.**
Uranotaenia balfouri, **430, 468.**
Uranotaenia bilineata fraseri, **467.**
Uranotaenia brevirostris, **90.**
Uranotaenia browni, sp.n., **70, 75–78, 85, 87, 94, 95, 96, 98, 100.**
Uranotaenia brumpti, **90.**
Uranotaenia cachani, **84, 92.**
Uranotaenia candidipes, **468.**
Uranotaenia civinskii, **278, 285, 288.**
Uranotaenia combesi, **90.**
Uranotaenia fusca, **90, 468.**
Uranotaenia grenieri, **90.**
Uranotaenia lavieri, **90.**
Uranotaenia lucyae, **468.**
Uranotaenia lutescens, **90.**
Uranotaenia mashonaensis, **468.**
Uranotaenia moultoni, **90.**
Uranotaenia nepenthes, **70, 71, 73–75, 87, 89, 90, 94, 96, 99, 100, 101.**
Uranotaenia nigripes, **468.**
Uranotaenia ornata, **90.**
Uranotaenia pandani (*pauliani*), **70–73, 74, 75, 76, 77, 87, 89, 90, 94, 96, 97, 98, 100, 101.**
Uranotaenia quadrimaculata, **89, 280, 281, 282, 285, 287, 288.**

Uranotaenia quinquemaculata, **90.**
Uranotaenia tsaratananae, **90.**
Uranotaenia tubanguii, **90.**
Uranotaenia xanthomelaena, **75.**
Uroplectes fischeri, **435.**
Urtica dioica (see Nettle).
usambarensis, Nasutitermes.

V.

vadschaggae, Microtermes.
vansomerenae, Aëdes vigilax.
Varanus niloticus, **426, 439, 508, 511, 512.**
vardoni, Adenota.
variegatum, Amblyomma.
Vegetable Marrow, persistence of DDT deposits on leaves of, **852, 853, 855, 856, 857.**
verbasci, Anthrenus.
verna, Aëdes leesoni.
versicolor, Trogoderma.
vexans, Aëdes (*Aëdimorphus*).
Vicia faba, Aphis fabae on, in Britain, **561–587**; used for rearing Aphids, **600.**
vigilax, Aëdes.
violacea, Necrobia.
virginica, Parcoblatta.
viridiscutum, Cheiloneurus.
vishnui, Culex.
vittatus, Aëdes (*Stegomyia*).
vivax, Plasmodium; Trypanosoma.
vorax, Anthrenus.
vulpinus, Dermestes (see *D. maculatus*).

W.

Wagtail, African Pied, **439.**
Wart-hog, **59, 518, 532, 533, 534, 536, 537.**
Waterbuck, **59, 518, 532, 533, 535, 536.**
Watercress, effect of mineral-deficient, on *Phaedon cochleariae*, **393–397.**
Wax Moth (see *Galleria mellonella*).
Wax Moth, Lesser (see *Achroia grisella*).
wayi, Pseudotheraptus.
Weaver-bird, **509.**
wellcomei, Anopheles.
weschei, Culex.
wesmaeli, Pristiphora.
westwoodi, Plastanoxus.
Wheat, *Agriotes* on, in Britain, **913–923.**
Wheat, Stored, pests in, and their control, **400–403.**
wigglesworthi, Culex (*Neoculex*).
Wireworms (see *Agriotes*).
Withius subruber, **700.**
Wolf Snake, Cape (see *Lycophidion capensis*).
woodi, Acarapis; Aëdes (*Stegomyia*).
Wuchereria, **280, 291, 292, 298.**
Wuchereria bancrofti, **284, 498, 515**; relation of mosquitos to, in Tanganyika, **419–436, 437–444, 495–504, 505–515.**

X.

xanthomelaena, Uranotaenia.
Xenopsylla crinita, **159, 170.**
Xylene, **852.**
Xylocoris flavipes, **662.**

Y.

Yellow Fever, **711, 738**; entomological studies relating to, in Kenya, **149–183.**

Z.

Zabrotes subfasciatus, **661, 663.**
zambesiensis, Odontotermes.
Zanzibar Protectorate, Coreids in, **221, 224, 225, 226, 233.**
zanzibarensis, Synacanthotermes.
Zebra, **518, 532, 534, 536, 537.**
Zeuxevania splendidula, **138.**
ziemanni, Anopheles coustani.
zombaensis, Culex.
zumpti, Ornithodoros.

INDEX TO NAMES OF PERSONS.

Abdalla, Swedi, **66.**
Abd el Hakim Kamel, **774, 779.**
Adamson, B. E., **311.**
Alexopoulos, C. J., **897.**
Allen, M. D., **393, 753.**
ap Griffith, G., **545.**
Armstrong, J. S., **294.**
Armstrong, Mrs. M. T., **666.**
Asperen, K. van, **837.**
Attia, R., **640.**

Babu Naidu, Mohan, **205.**
Bagster Wilson, D., **515.**
Bagster Wilson, Mrs. M. E., **436.**
Balfour-Browne, J., **666, 773.**
Balole, F., **502.**
Baltazard, M., **747.**
Banks, C. J., **561.**
Barlow, F., **547.**
Barnes, G., **19.**
Barnes, H. F., **37.**
Barr, A. R., **86.**
Basilewsky, P., **232, 240.**
Bax, S. Napier, **67.**
Belcour, J. Colas-, **747.**
Belkin, J. N., **277, 284, 288.**
Bell, G. T., **530.**
Beneke, E. S., **897.**
Benson, R. B., **749, 752.**
Bertram, D. S., **515.**
Bills, G. T., **625.**
Bondy, **809.**
Bordas, E., **559.**
Bradley, J. T., **103.**
Brett, G. A., **643, 666, 667, 832, 835.**
Brooks, A. C., **436.**
Brown, E. S., **69, 76, 79, 84, 86, 87, 92, 221.**
Brown, W. Burns, **191.**
Browne, J. Balfour-, **666, 773.**
Browning, E., **436.**
Bugher, J. C., **242, 255.**
Burges, H. D., **343, 344, 350, 773, 813.**
Burns Brown, W., **191.**
Bursell, E., **589.**
Burt, P. E., **39, 849.**
Burtt, B. D., **59, 66.**
Busvine, J. R., **301, 308.**
Buxton, P. A., **218, 308.**

Cain, A. J., **282.**
Cameron, E., **137.**
Cation, D., **897.**
Chaudhry, Ghulam-Ullah, **869.**
China, W. E., **238, 240, 436.**
Christophers, Sir R., **740.**
Clark, **284.**
Cobben, R. H., **845.**
Colas-Belcour, J., **747.**
Coombs, C. W., **350, 399.**
Cooper, B., **19.**
Crawford, M., **747, 748.**
Cunnington, A. M., **350.**
Currie, J. E., **666.**

Davey, J. T., **797.**
Davis, G. E., **747.**
Debenham, E. M., **666.**
De Lotto, G., **267, 269.**
Doncaster, J. P., **623.**
Donkelaar, C. van, **843.**
Dresden, D., **843.**
Drew, W. B., **897.**
Drion, E. F., **843.**
Dunn, J. A., **369, 389.**
Dupont, **103.**

Edmondson, C. H., **295.**
Edson, E. F., **701, 709.**
Eke, C., **367.**
Elton, C., **337, 350.**
Evans, H. E., **226.**
Evans, O., **436.**

Ford, J., **517.**
Fowler, V., **845.**
Fox Wilson, G., **845.**
Fraenkel, G., **795.**
Freegard, D., **276, 284.**
Freeman, G. H., **37.**
Freeman, J. A., **350, 399, 643.**
French, R. A., **193.**
Fryer, J. C. F., **103.**
Furlong, M., **463.**

Galbraith, I. C. J., **282.**
Gall, D., **362, 364, 367.**

Gamwell, H., **66.**
Gamwell, M., **66.**
Gardner, K., **700, 709.**
Garnham, P. C. C., **740.**
Geering, Q. A., **743.**
Ghulam-Ullah Chaudry, **869.**
Gillett, J. D., **241, 255.**
Glover, P. E., **57, 67.**
Golding, F. D., **226.**
Gowdey, C. C., **228, 267.**
Grandisson, A. G. C., **436.**
Greenslade, R. M., **709.**
Greenway, P. J., **436.**
Griffith, G. ap, **545.**
Grunberg, A., **803.**

Hadaway, A. B., **547, 773, 779, 781.**
Haddow, A. J., **761.**
Hall, D. W., **625, 644, 662.**
Hall, W. J., **240, 273.**
Hammond, J. H., **350, 666.**
Hamon, J., **84.**
Hanna, A. D., **669.**
Hardy, J. E., **797.**
Harley, J. M. B., **529.**
Harris, W. V., **135.**
Hartley, G. S., **709.**
Hayward, L. A. W., **666.**
Healy, M. J. R., **843, 913.**
Heath, D. F., **700.**
Heatherington, W., **669.**
Heisch, R. B., **740, 747.**
Helu, T. M. P. Kuli, **188.**
Herford, G. V. B., **795.**
Hesse, P. R., **127.**
Hinton, H. E., **666.**
Hocking, K. S., **530.**
Hoogstraal, H., **747.**
Hosni, M. M., **193.**
Howe, R. W., **350, 643, 773, 795.**
Hutson, R., **896.**
Hyde, M. B., **350, 835.**

Iyengar, M. O. T., **1, 9.**

Jackson, C. H. N., **57, 67, 517, 531.**
Jeffree, E. P., **753.**
Jenkins, Mrs. C. P., **586.**
Jewell, G. R., **530.**
Johnson, C. G., **586.**
Jones, T. Vaughan-, **67.**
Judenko, E., **669.**
Juldeh, G. M. F., **367.**

Kamel, Abd el Hakim, **774, 779.**
Kanakulya, W., **540, 545.**
Keen, Sir B., **545.**
Kemp, P. B., **113.**
Kenten, J., **599.**
Kerrich, G. J., **15.**
King, H. L., **897.**
Kirkland, R. C., **749.**
Kirkpatrick, T. W., **901, 911.**
Kredua, O., **709.**
Kuli Helu, T. M. P., **188.**

Laird, M., **185, 275, 291.**
Lambe, K. D., **640.**
Laurie, W., **515.**
Leeson, H. S., **443, 747.**
Le Pelley, R., **225, 240, 269, 271, 273.**
Loizides, P., **640.**
Lotto, G. De, **267, 269.**
Lumsden, W. H. R., **149, 476, 715, 740.**

McCrae, D. J., **272.**
MacDonald, A., **299.**
MacLean, J. A. R., **709.**
Malaise, R., **240.**
Mara, L., **559.**
Marks, E. N., **299.**
Mattingly, P. F., **1, 8, 9, 69, 436, 740.**
Menon, M. A. U., **1, 9, 10.**
Mer, G., **453.**
Merfield, F. G., **227.**
Michelmore, A. P. G., **273.**
Miles, H. W., **18, 25.**
Miles, M., **11, 21.**
Mohan Babu Naidu, **205.**
Moore, W. C., **807.**
Morison, G. D., **15, 753.**
Morrison, H., **271, 273.**
Mukerji, S., **774, 779.**
Munro, J. W., **781, 795.**
Murray, L., **753.**

Naidu, Mohan Babu, **205.**
Napier Bax, S., **67.**
Nash, T. A. M., **111, 357.**
Ndalo, A., **502.**
Ngashi, W., **502.**
Nickerson, B., **798.**
Nightingale, S. M., **350.**
Nixon, G. E. J., **37.**
Norris, J. D., **666.**
Notley, F. B., **899.**
Nzumbi, P., **502.**

Oldroyd, H., **436.**
Osae, **709.**
Osmond, D. A., **559.**
Ossiannilsson, F., **845.**

Page, A. B. P., **809.**
Parkin, E. A., **625.**
Paton, W. D. M., **218.**
Patterson, W. H., **226.**
Paulian, R., **73.**
Pearson, E. O., **240, 745.**
Peleg, J., **803.**
Pelley, R. Le, **225, 240, 269, 271, 273.**
Pilson, R. D., **597.**
Pinhey, E., **233, 240.**
Pitcher, R. S., **27.**
Pjatokova, M. V. L., **845.**
Pobeguin, **103.**
Polac'ek, K., **803.**
Potter, C., **54, 623, 843, 913.**
Pryor, M. G. M., **545.**

Ragge, D. R., **436.**
Raw, F., **913.**
Reid, J. A., **306.**
Remane, A., **845.**
Riley, J., **650, 666.**
Ripper, W. E., **709.**
Roberts, J. A., **367.**
Robertson, A. G., **57, 67, 597.**
Roblot, M., **802.**

Saliternik, Z., **445.**
Salt, G., **539.**
Séguy, E., **85, 103.**
Selman, I. W., **393.**
Smith, A., **419, 437, 495, 505.**
Smith, M. A., **436.**
Smith, S., **443.**
Snow, O. W., **709.**
Solomon, M. E., **189, 311, 586.**
Someren, Mrs. E. C. C. van, **88, 103, 174, 436, 463.**
Southwood, T. R. E., **845.**
Steinhaus, E. A., **744, 745.**
Stott, A. M., **350.**
Strong, W. M., **275.**
Styles, J. H., **749.**
Swaine, G., **225, 240.**
Swedi Abdalla, **66.**
Swynnerton, C. F. M., **59, 66.**
Symes, C. B., **54, 740.**

Teesdale, C., **463, 711.**
Thomson, W. E. F., **57, 67.**

Uvarov, B. P., **802.**

van Asperen, K., **837.**
Vanderplank, F.L., **224, 225, 233, 240.**
van Donkelaar, C., **843.**
van Someren, Mrs. E. C. C., **88, 103, 174, 436, 463.**
Varley, G. C., **240, 586.**
Vaughan-Jones, T., **67.**
Venning, J. H., **67.**

Ward, J., **39, 849.**
Way, M. J., **40, 224, 240, 852.**
Weiser, J., **747.**
Weitz, B., **436, 515, 531.**
Wharton, R. H., **301.**
Wijesundara, D. P., **10.**
Wilkinson, G., **224.**
Williams, C. B., **193, 586.**
Williams, E. A. B., **545.**
Williams, G. C., **666.**
Williams, J. C., **436.**
Wilson, D. Bagster, **515.**
Wilson, Mrs. M. E. Bagster, **436.**
Wilson, F., **273.**
Wilson, G. Fox, **845.**
Wirth, W. W., **297.**
Woodroffe, G. E., **350.**
Wright, D. W., **369, 389.**

Yesufu, Mallam H. M., **111, 367.**

Zolotarevsky, B., **802.**

4b/1 pl